The upper Silurian Downton Bone Bed of Weir Quarry, Herefordshire, England

Luke Matthew Hauser

The thesis is submitted in partial fulfilment of the requirements for the award of the degree of Doctor of Philosophy of the University of Portsmouth.

School of the Environment, Geography and Geosciences

United Kingdom

October, 2019

UNIVERSITY of PORTSMOUTH

“Science, my boy, is made of mistakes, but they are mistakes which it is useful to make, because they will lead little by little to the truth.”

From ‘Journey to the centre of the Earth’ by Jules Verne

“Fell deeds awake... Now for Wrath... Now for Ruin... and the Red Dawn...”

King Théoden, Lord of the Rings: The Two Towers

Dedicated to the loving memory of Arthur Douglas Cook and Doreen Alma Hauser, for their love and support during the course of the PhD. My only regret is they were unable to see me finish it.

Declaration

Whilst registered as a candidate for the above degree, I have not been registered for any other research award. The results and conclusions embodied in this thesis are the work of the named candidate and have not been submitted for any other academic award.

Luke Hauser, 2019

Word Count: 42,840

Abstract

The Downton Bone Bed is a multitaxic Fossil Concentration-Lagerstätte located in the Platyschisma Shale Member of the Downton Castle Sandstone Formation *c.*1.5m above the Ludlow Bone Bed. The Downton Bone Bed has received little direct study since its discovery over a century ago. This study focuses on the Downton Bone Bed from one locality, Weir Quarry (SO 4561 7520) on the Herefordshire/Shropshire border. The focus is to look at the palaeontology and sedimentology of the Downton Bone Bed, to understand how it formed and what fauna and flora is present in the bone bed providing new insights into the formation and palaeoenvironment of the bed. An integrated method of processing well-indurated bone beds was developed using paraffin impregnation and a microwave oven. The fossils of the Downton Bone Bed represent a restricted fauna and flora. Vertebrates comprise *Paralogania ludlowiensis*, *Thelodus parvidens*, *Gomphonchus* sp., *Nostolepis* sp. and *Onchus murchisoni*. *P. ludlowiensis* is the most common vertebrate in the Downton Bone Bed. There is also evidence to support the presence of an osteostracan and heterostracan. There are also three poorly preserved conodonts present. Organic walled fossils comprise *Cooksonia pertoni* /*Hollandophyton colliculum*, *Synorisporites downtonensis*, *Nematothallus pseudo-vasculosa*, *Prototaxites* sp. and *Pachytheca spherica*. Invertebrates are *Modiolopsis complanata*, *Turbocheilus helicites*, *Tunisiglossa*? *cornea*, *Lingula missendenensis*, *Frostiella groenvalliana*, *Londinia arisaigensis* and *Leperditia* sp. There is also evidence for eurypterids. The sedimentology provides evidence of two energy conditions shifting between a quiet low-energy setting, indicated by planar and quasi-planar laminations with trace fossils present (*Teichichnus* and *Planolites*) and periods of rapid burial in which all the body fossils were deposited. It is suggested here that the formation of the Downton Bone Bed was caused by storms. The environmental setting for the Downton Bone Bed is a lower shoreface of an epeiric sea, in proximity to a terrestrial freshwater source.

Table of contents

Appendices

List of tables

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 8

Table 8.2 Summary of Silurian bonebeds reviewed in this chapter.

List of figures

Chapter 1

Chapter 3

Text figure 3.21 Cut section of the DBB (DBBM 9), with the four horizons (1-4) present. Horizon 3 shows quasi-planar laminations and rip up clasts. Horizon 2 shows rapid deposition of sediment. The scale bar represents 1 cm.

Text figure 3.22 Example of syneresis cracks seen in the DBB on horizon 1 from sample DBBM 5. Scale represents 1 cm.

Text figure 3.23 Examples of the Downton Bone Bed from Weir Quarry; sample points 5 and 6 illustrating the richness of the bonebed; thelodont (Th) denticles are visible in these thin sections.

Text figure 3.24 Examples of the Downton Bone Bed from Weir Quarry; sample points 7 and 6 illustrating the richness of the bonebed; including thelodont denticles (Th) and an acanthodian spine (Ac).

Text figure 3.25 DBBM 9 with two close-ups showing how inconspicuous some of the vertebrate fossils (arrows) are within the bed, illustrating that they can easily be overlooked.

Text figure 3.26 Allen and Tarlo's (1963) text figure 2 of the Downton Castle Sandstone Group and their interpretation.

Text figure 3.27 Logs modified from Allen's (1974) frig. 21 of sections taken from two localities, of significance to this study; (b) upper part of the formation, quarry near Downton Castle (SO 447750) and (c) upper part of formation, quarry near Downton Castle (SO 455751).

Chapter 4

.

Text figure 4.17 Selection of thelodont body forms (modified from Ferrón and Botella, 2017): A, *Turinia pagei* in dorsal view. B, *Lanarkia horrida* in dorsal view. C, *Loganellia scotica* in dorsal view. D, *Phlebolepis elegans* in lateral view. E, *Sphenonectris turnerae* in lateral view. F, *Furcacauda heintzae* in lateral view. G, *Pezopallichthys ritchiei* in lateral view (Original outlines, A, B and C Märss & Ritchie 1998; D from Ritchie 1968; E, F, G modified from Wilson & Caldwell 1998).

Text figure 4.18 Patterns of denticle coverage and their function on the two closest taxa to *Paralogania ludlowiensis* (B-E) and *Thelodus parvidens* (G-H). Also included are the two modern analogues for the ecology that their squamation suggests. A, Schooling species of low to moderate speed (illustrated by *Squalus acanthias*). B, *Shielia gibba*. C, *Shielia parca*. D-E, *Shielia taiti*. F, Demersal species on sandy and muddy substrates (illustrated by *Scyliorhinus canicula*). G, *Thelodus laevis*. H, *Thelodus macintoshi*. Scale bars represent 1cm; modified from Ferrón and Botella (2017).

Text figure 4.19 Palaeogeographical map with the locations of the *Thelodus parvidens* communities (Turner 1999), illustrating the ability for the community to spread across the region. CF Caledonian front; TS, Thor suture; IS, Iapetus Ocean suture (Modified from Torsvik and Cocks 2016).

Text figure 4.20 Figure 1 from Baarli et al. (2003); their interpretation of the Baltica continent during the middle Silurian.

Chapter 5

Text figure 5.1 Faunal list produced by Elles and Slater (1906): red box indicates the fauna associated with the Platyschisma-Bed which included the DBB.

Text figure 5.2 Faunal list produced by Elles and Slater (1906): red box indicates the fauna associated with the Platyschisma-Bed which included the DBB.

Text figure 5.3 The lithological and faunal succession, from locality 3.2b on the N side of Whitcliffe Road, Ludlow (modified from fig. 38 in Siveter et al. 1989). Approximately 1.5 m above the base of the LBBM is an assemblage that appears to be an indicator of the DBB.

Text figure 5.4 *Modiolopsis complanata*: close-up of specimen DBBM1; growth lines can be seen across the oxidised surface. The scale is 1 cm per division.

Text figure 5.5 Close-up of DBBM4, note the white/cream coloured material at the top of the image, possible preservation of shell. Scale represents 1 cm.

Text figure 5.6 External mould of *Londinia arisaigensis* (Copeland 1964) showing a possible brood pouch. Scale bar represents 500 µm.

Text figure 5.7 DBBM3, bedding surface with numerous *Modiolopsis complanata* as internal and external moulds Scale is 6 cm.

Text figure 5.8 The two best-preserved specimens of *Turbocheilus helicites* DBBM 5; scale bars represent 6 mm for the top image and 7 mm in the bottom image.

Text figure 5.9 DBBM9 *Leperditia* sp. scale is 1 mm.

Text figure 5.10 Possible eurypterid chelicera; DBBM 7 images taken in different orientations, and with light at differing oblique angles showing different details. The scale is 3 mm.

Text figure 5.11 Salter's (1852) illustration of a denticle from the chelicera of *Pterygotus problematicus* (Agassiz, 1839), now *Erettopterus megalodon* (Kjellesvig-Waering, 1961); the dotted line represents the outline of DBBM 6 and 7; a scale was not provided by Salter (1852).

Chapter 6

Text figure 6.12 storm sedimentation model suggested by Richardson and Rasul (1991) (taken from Allen 1985, fig. 13.34)

Text Figure 6.13 Palaeoenvironments in the Welsh Borderland region during the late Silurian copy of Turner et al. 2017 fig. 9).

Chapter 7

Text figure 7.1 Antia's plate 1 from his 1979 PhD thesis showing "*Thelodontites corftonensis".* A) *Gomphonchus tenuistriata* fragment with "*T. corftonensis*" boring in its grooves. (Distance between adjacent grooves = 250-300 µm). B) Borings on a phosphatized fragment of *Serpulites* sp. (Boring diameter = 10-15 µm) C) "Holotype" of "*T. corftonensis*" (arrowed) on the illustrated (Plate 1A) specimen of *G. tenuistriata*. Recent *Thelodontites* boring (diameter 30 µm) from Sales Point, Bradwell, Essex. E) Algal form B boring of Antia (1979a) on a *Thelodus parvidens* scale. Note the weathering stage 1 cracks (cf. Antia, 1979a) diameter of borings = 10-15 µm.

Text figure 7.2 Ichnofabric indices, indicating the amount of bioturbation (taken from Droser & Bottjer 1989).

Text figure 7.3 Top: An image of the Weir Quarry section. Middle: overlay of sample collection points within the Weir Quarry section. Bottom: variation in bioturbation index of the DBB across the section. F= fault.

Text figure 7.4 Graphs of each horizon's B.I., across the 8 m of lateral exposure at Weir Quarry with the sample points 1-19; as only a small amount of 10 could be collected it is omitted.

Text figure 7.5 Graph of ichnofossil diversity and abundance across the section at Weir Quarry. Note that this records only identifiable ichnotaxa, so despite some points showing zero trace fossils this does not mean they are devoid of them.

Chapter 8

Chapter 9

Text figure 9.1 Map of the Baltic Sea (modified form NormanEinstein wiki commons 2006) table below indicating the diversity of marine groups in different parts of the Baltic Sea (modified from Segerstråle, 1957).

Text figure 9.2 Graph showing the total diversity of groups seen in the DBB.

Text figure 9.3 Ecological composition of fauna and flora in the DBB, showing life position of taxa (modified from Siveter 1984): 1, organic-walled macrofossils. 2, trace fossils. 3, *Turbocheilus helicites*. 4, leperditiids. 5, eurypterid (Hughmilleriidae). 6, lingulate brachiopods. 7, *Modiolopsis complanata*. 8, *Londinia arisaigensis*. 9, thelodont. 10, acanthodian. 11, eurypterid (Pterygotidae).

Text Figure 9.4 Facies model for a marine shoreline environment (taken from Tucker 2003).

Text figure 9.5 The Downton Sea during the mid Ludfordian, this environment represents the environment adjacent to the lower shoreface where the DBB was deposited 1) acanthodian, 2) eurypterid, 3) *Thelodus parvidens*, 4) *Modiolopsis complanata*, 5) *Sclerodus* pustuliferus, 6) *Paralogania ludlowiensis* and 7) *Archegonaspis* sp. (artwork by Dr Mark Witton).

Text figure 9.6 Coast of Downton Sea during the mid Ludfordian, 1) Localized low temperature wild fires, 2) Downton Sea, 3) Rivers flowing into the Downton Sea, 4) Variety of early plants such as *Cooksonia* and 5) The fungus *Nematothallus* (artwork by Dr Mark Witton).

Text figure 9.7 Map showing extent of the nineteen DBB localities in the U.K., the red marker indicates Weir Quarry (modified from Digimap 2019).

List of plates

Chapter 2

Examples of ostracod peel experiments on the DBB. A) mould of *Londinia arisaigensis as is found on bedding plane of the DBB. B) Londinia arisaigensis* heteromorph DBB18 500 3, extracted using paraffin expansion method. C) DBB1 cast used liquid latex. D) *Londinia arisaigensis* Millitest 1, cast using Milliput® standard. E) *Londinia arisaigensis* DBB1, cast using Milliput® superfine. F) *Londinia arisaigensis* DBB7, cast using PRESIDENT regular body A-silicone. G) Brachio1 fragment of lingulate brachiopod on the surface of the DBB, cast using PRESIDENT regular body A-silicone. H) Brachio1 close up of Brachio1 showing growth lines and ornamentation, cast using PRESIDENT regular body A-silicone. Scale equals 100 µm A-G, H equals 20 µm.

Chapter 3

Explanation of Plate 3.1 Thin sections of each horizon (1-4) of the Downton Bone Bed in stratigraphical order; left-hand side is in PPL (Plain Polarized Light) and right is in XPL (Crossed Polarized Light).

Explanation of Plate 3.2 Cut sections of DBB at Weir quarry, samples from collection points 1-3. 1) Swaley cross stratification present with well-defined laminations, but no fossils present. 2) Has all four horizons with the bone bed being deposited in between horizons 1 and 2; 2 and 3; 3 and 4. Horizon 3 shows the typical planar laminations, while horizon 4 has wavy laminations. 3) dominated by horizon 2, with wavy laminations. The fossils are deposited on the top of horizon 2. Scales represent 1cm.

Explanation of Plate 3.3 Cut sections of DBB at Weir quarry, samples from collection points 4-6. 4) all four horizons are present, although horizon 1 is very thin. The thickest horizon is horizon 3 which again shows planar laminations, the laminations that were present in 4 have been lost to bioturbation while fossils are mostly confined to horizon 2. 5) The four horizons are still present; however, horizon 1 is now very thin. Horizon 2 still contains many fossils, while horizon 3 has planar laminations with swaley cross beds at the top. 6) At this point horizons 3 and 4 are missing while horizon 1 has increased in thickness and displays planar laminations, horizon 2 has an erosive base, the horizon is full of fossils. There are several cross-sections of the gastropod *Turbocheilus helicites*. Scales represent 1 cm.

Explanation of Plate 3.4 Cut sections of DBB at Weir quarry, samples from collection points 7-9. 7) The four horizons are now present. Horizon 1 has thinned out, and at the interface between horizons 1 and 2 a significant amount of vertebrate material is present. 8) This is an incomplete bed as can be seen by the irregular lower surface, this, however, is the best example of sample point 8 in the material collected from Weir Quarry. Horizon 2 would likely continue down, though it is unclear if horizon 1 would be present. 9) Only the upper two horizons are present; the bed is dominated by horizon 3, which shows planar laminations. Scales represent 1 cm.

Explanation of Plate 3.5 Cut sections of DBB at Weir quarry, samples from collection points 11-13. 11) Is an incomplete bed, the upper horizons 3-4 are not present. Horizon 1 is homogeneous silt, while horizon 2 has an angled erosive base and represents a sharp change in sedimentary input. At the boundary between horizons 1 and 2, vertebrate fossils are seen. Horizon 2 has planar laminae. 12) Continues to show only the lower 2 horizons although the thickness of the bed has greatly increased, horizon 1 is still homogeneous silt with a planar laminated rip-up clast in the lower left-hand side. Horizon 2 also shows a mud rip-up clast in the lower section. However, there are few laminations with the rest of the horizon, as it partly looks as if bioturbation has taken place near the top of the bed. 13) The four horizons return, and the overall thickness of the bed decreases. Horizons 1 and 2 are very thin and horizon 2 has an erosive base once again. Horizon 3 displays more planar laminations and is the thickest horizon. Horizon 4, like horizons 1and 2, is very thin.

Only a few vertebrate fossils are seen at the interface between horizon 3 and 4. Scales represent 1 cm.

Explanation of Plate 3.6 Cut sections of DBB at Weir quarry, samples from collection points 14-16. 14) Horizon 4 is absent at point 14. However, horizon 1 has increased in thickness and shows planar lamination as well as numerous trace fossils, while horizon 2 is bioturbated with oxidised material (likely shell fragments). This horizon contains all of the fossils preserved in this sample. Horizon 3 has a reduced in thickness has more silt that is common in this horizon. Quasi-planar laminations are present. 15) The bed is thin and is missing the fourth horizon. Horizon 2 has an erosive base, and the fossil material is aggregated at the interface between horizon 1 and 2. Horizon 2 is consistent with planar laminations. 16) Is a generally featureless bed with only two horizons, horizon 3 does have planar laminations. Scales represent 1 cm.

Explanation of Plate 3.7 Cut sections of DBB at Weir quarry, samples from collection points 17-19. 17) The bed thickness has once again increased and only horizons 2 and 3 are present. At the interface between 2 and 3 fossils are present. 18) The bed has thinned; only horizons 1 and 2 are present. Horizon 1 has planar laminations as well as many trace fossils, while horizon 2 is structureless and has oxidised material mixed in with vertebrate material. 19) The bed is similar from the last sample point as only horizons 2 and 3 are present. However, horizon 1 has become thicker and is even more bioturbated than 18. Finally, horizon 2 is rich in fossil material but is structure less. Scales represent 1 cm.

Chapter 4

Explanation of Plate 4.1 Figs A-R *Paralogania ludlowiensis* (Gross, 1967): trunk scales, A) DBB5.500.1, B) DBB4.500.4, C) DBB4.500.4, D) DBB4.500.5, E) DBB6.500.1, F) DBB4.500.2, G) DBB20B.500.4, H) DBB20.500.1, I) DBB.500.f, J) DBB20.500.28, K) DBB5.500.8, L) DBB20.500.16, M) DBB20.500.22, N) DBB5.500.1a, O) DBBF.500.4, P) DBB20.212.1, Q) DBB20.500.2, R) DBB20.500.41. A,C-D, F-J, Q-R, in crown view. B, E, O, in lateral view; K, N, oblique lateral view of neck; L, and P, oblique lateral view of the crown. Scale bars

represent 100 µm, Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

Explanation of Plate 4.2 Figs A-R *Paralogania ludlowiensis* (Gross, 1967) trunk scales, A) DBB20.500.30, B) DBB20.212.7, C) DBB20.500.33, D) DBB.500. j, E) DBB.500.v, F) DBB.500.z, G) DBB30B.212.2, H) DBB7.212.7, I) DBB20B.212.3, J) DBB5.212.10, K) DBB.212.au, L) DBB.212.bj, M) DBB5.212.2, N) DBB5.212.1, O) DBB.212.19, P) DBB.212.13, Q) DBB.212.6, R) DBB18.212.2. A, C, E, L, N, O and R in crown view; I and Q in lateral view; B, D, F, J, K, M and P oblique lateral view of neck; G, oblique lateral view of the base; H in base view. Scale bars represent 100 µm; Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

Explanation of Plate 4.3 Figs A-I *Paralogania ludlowiensis* (Gross, 1967), A) DBB4.212.1, B) DBB4.500.3, C) DBB.212.br, D) DBB5.500.3, E) DBB20.500.23, F) DBB19.500.3, G) DBB.212.j, H) DBB.212.r, I) DBB.500.U. A-F possible *Paralogania* sp. transitional scales; G-I head scales. J-N *Thelodus parvidens* (Agassiz, 1839), J) DBB.212.17, K) DBB.212.2, M) DBB5.212.4, DBB20.500.6, trunk scales. A, D, F, J in crown view; B in oblique lateral view of the base; C and N in oblique lateral view of neck; E in base view; G-I and K-M in lateral view. Scale bars represent 100 µm, Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

Explanation of Plate 4.4 *Gomphonchus* sp. A-B) WQ2a.212.G, C) DBB20.500.40, *Nostolepis* sp. D) DBB4.212.1, E) DBB5.500.h, indeterminate Acanthodii material F) DBB5.212.1, denticle. G) WQ1b.G, H) WQ1a1.212.H, I) DBB20.500.2, J) DBB4.500.2a, K) DBB.212.q, L) DBB5.500.1, M) DBB14.5.500.1, fin spine fragments. N) DBB19.500.5, O) WQ1A1.212.b tooth whorl fragments. A, F, G, I, L, M lateral view; B-D; oblique lateral view of the crown, E oblique lateral view, H, J; oblique lateral view of the tooth; tooth view O, K; dorsal view of fin spine. Scale bar represents 100 µm.

Explanation of Plate 4.5 Macro specimens of acanthodian spines found in the DBB: A-B *Onchus murchisoni* (Agassiz, 1837); C-D indeterminate fin spine side and counter side *Acanthodii* indet. A) DBBM 1 lateral view B) DBBM 2 lateral view C) DBBM 12 dorsal view D) DBBM 13 dorsal view.

Chapter 5

Explanation of Plate 5.1 Fig. A-D fragments of *Tunisiglossa*? *cornea* Cocks and Popov; E, H-K fragments of *Lingula missendenensis* Straw with Ea a close-up of E showing ornamentation on the shell. F-G near complete valve of *Lingula missendenensis* Straw. A) DBB5 500 4 B) DBB20 500 2 C) DBB5 500 2 D) DBB5 212 3 E) S212z2 Ea) S212z2a F) DBB19 500 2 G) DBB19 500 2 H) DBB20 500 4 I) DBB20 500 5 J) DBB20 500 1 K) DBB7 212 1. A-K in Oblique lateral view. Scale bars represent 100 µm.

Explanation of Plate 5.2 Figs A-C *Frostiella groenvalliana* Martinsson A) tecnomorph DBB20B 500 1 B) tecnomorph DBB7 500 1 C) tecnomorph DBBM8 1. D Non-palaeocope D) DBB18 500 1. E-L *Londinia* cf. *arisaigensis* Copeland E) heteromorph DBB18 500 3. F) tecnomorph DBB18 500 2. G) tecnomorph DBB14.5 500 1. H) tecnomorph DBBM8 2. I) tecnomorph DBB8M 3. J) tecnomorph DBB8M 4. K) tecnomorph DBB8M 5. L) tecnomorph DBBM8 6. A-D, G-L lateral view. E-F oblique lateral view. Scale bar represents 100 µm. A-B, D-G internal casts from Paraffin expansion method, C, H-I and L external casts using Coltene 4823, Type 2, medium consistency Polyvinylsiloxane J-K Milliput® Superfine white.

Chapter 6

Explanation of Plate 6.1 *Cooksonia pertoni* Lang; sporangia from the DBB at Weir Quarry, in lateral view. A) DBB 53 b; Aa) close up of A; B) DBB500 b; Ba) close up of B; C) DBB500 c; D) DBB6 53 4; E) DBB16 500 1; F) DBB15 500 1; G) DBB1 500 1; H) DBB5 53 4; J) DBB1 53; I) DBB4 53 5. Scale bars represent 100 µm for A-G, 20µm for H and J and 10µm for I.

Explanation of Plate 6.2 Eutracheophytes and allies from the DBB at Weir Quarry. A-G Axes of *Cooksonia pertoni* Lang; H-I Axes of *Hollandophyton colliculum* Rogerson, Edwards, Axe and Davies? A) DBB14 500 1; B) DBB3 53; C) DBB5 500 2; D) DBB5 53 1; E) DBB5 500 1; F) DBB6 53; G) DBB2 53 3; H) DBB5 500 2; J) DBB9 500 1; K) DBB2 53; I) DBB8 500 1. The scale bars represent 100 µm except for K where it is 20 µm.

Explanation of Plate 6.3 Eutracheophytes and nematophytes found in the DBB at Weir Quarry A *Synorisporites downtonensis* Richardson and Lister? B-G *Nematothallus pseudo-vasculosa* Lang H-I *Prototaxites* sp. J-Kb *Pachytheca sphaerica* Hooker. A) DBB 53 d; B) DBB 53 I; C) DBB6 53 11; D) DBB6 53 6; E) DBB2 500 41; F) DBB7 53; G) DBB5 53 3; H) DBB 500 a; I) X DBB81 53; J) DBB20 500 2; K) DBB20 500 1; Ka) DBB20 500 1a close up of K; Kb) DBB20 500 1c close up of K. The scale is 100 µm for A-C, E, H, J-K. 20 µm for D, F-G, I and Ka, 10 µm for Kb.

Explanation of Plate 6.4 Organic-walled fossils from the DBB at Weir Quarry A, phytoclast, B-C possible fungal hyphae, D-J unidentified material. A) DBB 10a 53; B) DBB2 500 11; C) DBB13 500 1; D) DBB3 53 7; E) DBB7 53 4; F) DBB4 53 6; G) DBB9 53; H) DBB7 53 7; I) DBB5 53; J) DBB21 53. The scale is 10 µm for A, F-H, 100 µm for B-E and J, 20 µm for I.

Chapter 7

Explanation of Plate 7.1 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 1-3. The scale represents 1cm.

1) B.I. 1. No trace fossils present

2) B.I. 2. *Teichichnus* sp. is present in the middle of the bed, while *Planolites* sp. can be seen in the top of the bed.

3) B.I. 1. No trace fossils present.

Explanation of Plate 7.2 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 4-6. The scale is equal to 1cm.

4) B.I. 3. *Teichichnus* sp. and *Planolites* sp. are present in the middle of the bed; the top of the bed shows extensive bioturbation.
5) B.I. 2. *Teichichnus* sp. and *Planolites* sp. are present only in the middle of the bed.
6) B.I. 2. *Teichichnus* sp. is present in the lower part of the bed.

Explanation of Plate 7.3 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 7-9. The scale represents 1cm.
7) B.I. 2. Extensive bioturbation in horizons at top and bottom of the bed. No ichnogenera can be identified.
8) B.I. 3. *Teichichnus* sp. and *Planolites* sp. are present in the middle of the bed the top of the bed shows extensive bioturbation.
9) B.I. 3. *Teichichnus* sp. and *Planolites* sp. in the lower part of the bed, with a large example *Teichichnus* sp. on the right-hand side, with clear spreiten structures. Extensive bioturbation at the top of the bed.

Explanation of Plate 7.4 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 11-13. The scale represents 1cm.
11) B.I. 1. No trace fossils present.
12) B.I. 3. Extensive bioturbation is seen in the upper part of the horizon; no ichnogenera can be identified.
13) B.I. 2. Bioturbation is seen in the lower and upper parts of the bed, *Teichichnus* sp. present.

Explanation of Plate 7.5 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 14-16. The scale represents 1cm.
14) B.I. 3. Extensive bioturbation throughout the bed; good examples of *Teichichnus* sp. are seen in the lower part of the bed.
15) B.I. 1. No trace fossils present.
16) B.I. 1. No trace fossils present.

Explanation of Plate 7.6 Cut sections of DBB at Weir Quarry showing B.I., samples from collection points 17-19. The scale represents 1cm.

17) B.I. 2. There is slight bioturbation at the top of the bed, with only *Teichichnus* sp. being seen.

18) B.I. 4. The lower part of the bed shows examples of *Teichichnus sp. and Planolites* sp.

19) B.I. 4. The lower part of the bed shows examples of *Planolites* sp. while the upper shows many *Teichichnus* sp.

Explanation of Plate 7.7

A) Thin section of DBBI15 with traces present in horizon 3; all traces are *Teichichnus* sp. (Te). The scale represents 1 cm.
B) Thin section of DBBI13 with traces present in horizon 3; traces are *Teichichnus* sp. (Te) and *Planolites* sp. (Pl). The scale represents 1 cm.

Explanation of Plate 7.8

A) Thin section of DBBI12 with traces present in horizon 3; traces are *Teichichnus* sp. (Te) and *Planolites* sp. (Pl). The scale represents 1 cm.
B) Thin section of DBBI14 with traces present in horizon 3; all traces are *Teichichnus* sp. (Te). The scale represents 1 cm.

Abbreviations

A	Acanthodian
AC	Acanthodian spine
B.I.	Bioturbation index
CC	Central cavity
CF	Caledonian front
DBB	Downton Bone Bed
DBS	Downton Bone Sand
DCF	Downton Castle Formation
DCSF	Downton Castle Sandstone Formation
D.O.M	Dispersed Organic Material
DT	Dentine tubules
GSM	British Geological Survey
I.C.D	Ichnofabric constituent diagram
I.I.	Inshore index
IS	Iapetus Ocean suture
KV	Kilovolts
LBB	Ludlow Bone Bed
LBBM	Ludlow Bone Bed Member
MB	Missing bone
M.I.I	Marine inshore index
NHM	Natural history museum
NMW	National Museum of Wales
PC	Pulp cavity
Pl	*Planolites*
PPL	Plane polarized light
PSM	Platyschisma Shale Member
RBB	Rhaetian Bone Bed
SEM	Scanning electron microscope
SG	Specific gravity
SL	Superficial layer
SM	Sandstone Member
T	Thelodont

TBB	Temeside Bone Bed
Te	*Teichichnus*
TEM	Transmission electron microscope
Th	Thelodont denticle
TS	Thor suture
UWF	Upper Whitcliffe Formation
VC	Vascular cavity
XPL	Cross Polarized Light

Dissemination

Papers in peer-reviewed journals

Hauser, L. M. (2016). An integrated microwave technique for releasing microfossils from an indurated bone bed. *Journal of Micropalaeontology*, *35*(1), 62-65.

Conference presentations

Hauser, L. M. (2017). The Downton Bonebed: insights into a lost world. 61st Palaeontological Association annual meeting, Imperial college London, U.K. 2017. Oral.

Hauser, L. M. (2015). The Downton "Tooth Bed": a lost world. 63rd Symposium of Vertebrate Palaeontology and Comparative Anatomy, Southampton, U.K. 2015. Oral presentation.

Hauser, L. M. (2015). Breaking bad…bone beds: processing the Downton Bone Bed. 24th Symposium of palaeontological preparation and conservation with the Geological Curators' group, Southampton, U.K. 2015. Oral presentation.

Hauser, L. M. (2014). Vertebrates of the Downton Bone Bed. *4th IGCP 591 the early to middle Paleozoic revolution annual meeting, Tartu, Estonia 2014*. Poster presentation.

Hauser, L. M. (2013). The Palaeontology and Sedimentology of the Downton Bone Bed. *3rd IGCP 591 the early to middle Paleozoic revolution annual meeting, Lund, Sweden 2013.* Poster presentation.

Hauser, L. M. (2012). The Palaeontology and Sedimentology of the Downton Bone Bed. 60th *Symposium of vertebrate palaeontology and comparative anatomy, Oxford, U.K. 2012.* Poster presentation.

SEES postgraduate research day presentations

Hauser, L. M. 2015. Palaeontology and sedimentology of the Downton Bone Bed. Oral Presentation.

Hauser, L. M. 2014. Palaeontology and sedimentology of the Downton Bone Bed. Oral Presentation.

Hauser, L. M. 2013. Palaeontology and sedimentology of the Downton Bone Bed. Oral Presentation.

Hauser, L. M. 2012. Palaeontology and sedimentology of the Downton Bone Bed. Oral Presentation.

Outreach Events

Hauser, L. M. 2018. I have a bone to pick with you: The Science of bonebeds. Oral presentation. *Pint of Science* 2018.

2018 Portsmouth Grammar School. *Dinosaur talk to year 1 classes*.

2011 Blast from the past. *University of Portsmouth stand*.

2011 Thyreophora: the shield bearers. Southampton Geological Society

Acknowledgements

There are many people I would like to thank for their contributions towards the completion of this body of work.

I would first like to thank my first supervisor Dr David K. Loydell. It would be fair to say that I owe David a great deal, though he would never accept how much he has helped and inspired me to be a better scientist. He would simply claim that he was "just doing my job", but from the moment I started as an undergraduate in 2008 he has always helped me when I asked him or needed him, and during the PhD he has been a constant source of knowledge and wisdom, and when I was coming apart at the seams with stress, his constant calmness always reassured me that I could finish and to keep my focus. Oh and not forgetting his trusty red pen.

I also thank my second supervisor Prof. David M. Martill. Dave has always been a mentor to me, in part because he works on the groups of fossil organisms that I wish to work on, but more so, Dave has also struggled with dyslexia. He, however, overcame these challenges and has become a respected expert in his field. Like David, he has always supported and encouraged me from when I was an undergraduate, in particular when he was my dissertation tutor during my third year. I have been lucky enough to publish a paper with Dave which gave me the experience I needed to publish in the future.

My third supervisor, Dr Tiiu Märss, is also thanked. During 2012 I was lucky enough to visit her in Tallinn, Estonia. She welcomed me and immediately made me feel comfortable in both her country and her department. Although I only spent a week with her, I learnt so much and throughout my PhD, she would always answer my email questions. My only regret is that I could not work more closely with her during my PhD on other projects.

Before I thank anyone else I wish to say that it is no exaggeration that without these three supervisors I would not have written this PhD thesis, and for that, I am eternally grateful. They all have contributed to making me a better researcher than I

was when I started and in the years to come I hope that I can grow further, as a way of thanking them for all their time and patience.

Special mention goes to all the technical support I have had over the course of the PhD. I thank Elaine Dyer for support with the SEMs (all three of them!) as well as helping me perfect my paraffin expansion method (we only set fire to 2 boxes!) and processing some of my paly samples. Thanks are also given to Richard Hing, for various technical help over the years as well as for some excellent conversations. Geoff Long I must thank not only for cutting all my many thin and thick sections, and cross sections but also doing so throughout my time as an undergraduate. I thank Dr Anthony Butcher for a great many things, in particular, though for processing many of my paly samples and for technical support and discussion on various Silurian things (and Star Wars). Dr Mark Witton is thanked also for advice support and creating exceptional artwork for this thesis.

I want to thank all of the many postgraduates in SEGG for their support, there are far too many of you guys to thank individually. Special thanks go to Mike O'Sullivan and Nathan Barling; we started our journey together in 2008 and although we're now apart it was an honour to see you both develop as researchers. I also thank Georgia, Holly, Emily, Glenn, Adam, Ali, Natalia, Sean, Mike and Orla for making the office just that little bit nicer to be in (long live ice cream Fridays). A mention is also required for two of the more recent arrivals in the SEGG PhD family, Roy and Simon, both of who I had the pleasure to teach as undergraduates and are now in the department. They have brought a passion and energy to the department that I have certainly appreciated, helping me to get across the final stages of my project.

Special mention goes to Chris Tait, who started my academic journey with me, Nathan and Mike in 2008. Since then we have become close friends and if I have ever needed to bounce ideas, rant about issues I have encountered during the PhD, or need an extra pair of hands in the field. Chris has always been there for me and for Emma, and I am eternally grateful for all his support and wise council over the decade we have known each other.

During my time researching for this thesis I have visited many museum collections, so I wish to thank the many establishments who have helped me with various collections: Emma Bernard and photographers Aimee McArdle and Kevin Webb at the Natural History Museum, London; Dr Stig Walsh for liaising with The National Museum of Scotland, Edinburgh; Abigail Cox at The Ludlow Resource Centre, Ludlow; and Matthew the Sedgewick Museum, Cambridge. I wish to thank all of the following people for assisting me with access to Downton Gorge so that I could conduct field work: Simon Cooter of the Downton Gorge nature reserve, Sue Buckingham from Natural England and Emma Tolley from the Downton Estate. I would also like to than Dr Alexander Weh and Selfrag for allowing me to have sample processed free of charge.

I have also been lucky enough to speak with many excellent research scientists who have helped me: Dr Carole Burrow, Dr Robin Cocks, Dr Giles Miller and Dr Susan Turner. There are many others who I hope can forgive me omitting their names but I count myself very lucky to have been in contact with so many great scientists over the duration of this PhD.

I would now like to thank my family without whom none of this would have been possible. To my mother and father; I do not know how to write this, I do not know the words to use to convey my gratitude for all you have done for me over not just this PhD, but my life, you both brought me into this world and with that gift I hope this in some way tells you how much I appreciate you both by trying to overcome my shortcomings and to make you both proud. At this point, you will look up as you read this and say “we have always been proud of you”. I know this of course, but you have always been my role models; loving, kind, strong, and wise, always making me proud of you both. On top of this you have taken on the burden of helping me fund my studies when you know that I could never truly pay you back, you have allowed me to follow my dreams without hesitation and for that, I can never truly tell you how much I love you both, thank you.

To my Sister Laura, well here we are after 8 years and your brother has finally finished. I am not sure if I have ever told you this but you are one of my biggest role models. Every day in your job you go and help people and work long hours with

little thanks; that is a quality I have always admired. You have always inspired me to work harder to aim higher than I thought I could. When were at school I was always told by teachers how bright you were (which I'm sure confused them, as to why I struggled so much) but I knew that although you are bright you had a much rarer gift and one I have always respected, you have always been a hard worker, you have never settled for good enough; you always have pushed yourself to be better, and that has stuck with me. Hopefully, this thesis will show you how much I have appreciated your work ethic, your support and ability to make me laugh, thank you.

Finally, I wish to thank my wife Dr Emma Hart, When I started my PhD journey in 2011, I was going to get my head down and focus for however long it took on my PhD. In hindsight, I'm glad I looked up from my work, because I can't imagine my life without her. They say in life you have a path laid out in front of you and if you are lucky your path will cross with someone you can share your life with. I must be particularly lucky as not only have our paths crossed but we now walk the same path. She is my rock (no pun intended!) but she has never left my side, always there with support and advice. She loves me unconditionally and I cannot explain here how that makes me feel, when I have had a bad day, when I have had to go to work instead of working on my PhD, she always knows how to make me feel better. Never asking for anything but my love and support, I give it willingly. She is my everything, the reason I want to carry on in this field when others decide to take easier paths. She is my inspiration as a young researcher. Emma has had to overcome many hurdles already in her career but she has done them with grace and dignity. She makes me want to work harder at my craft so I can be just a fraction of the scientist she is. I thank her here for she is one of the main reasons I knew I could complete this, what has at times felt like a herculean task, her unwavering faith in me and my ability and knowledge is a constant source of strength. I wish I had the ability to explain how Emma makes me feel, but all I can say is that she is as vital to me as the air I breathe, and without her, I would be lost, I thank you, Emma, for everything and so much more besides.

Thesis structure

This thesis on the upper Silurian Downton Bone Bed of Weir Quarry comprises nine chapters of unpublished research carried out over the course of this study. Each of the main chapters (not including the introduction) contains a separate previous work section and all of the conclusions are discussed in the final chapter.

Chapter 1 provides an introduction to the thesis with a focus on bone beds, The Silurian and the Downton Bone Bed; this chapter also contains the aims of the study and contribution of the research. **Chapter 2** discusses the methods used in this thesis. In **Chapter 3** the sedimentology is described of the section studied as well as discussions on the wider area. **Chapter 4** describes and discusses the vertebrates found in the Downton Bone Bed. In **Chapter 5** the invertebrates found in the Downton Bone Bed are described and their significance is discussed. **Chapter 6** contains descriptions of the organic-walled plant, fungi and allies contained in the Downton Bone Bed with further discussions. **Chapter 7** comprises a brief description of the ichnofauna of the Downton Bone Bed; their diversity and its importance are discussed. In **Chapter 8**, a review of Silurian bone beds is given followed by discussion on their significance. **Chapter 9** provides conclusions based on all the previous chapters focusing on the palaeoecology and palaeoenvironment, as well as suggestions for further work.

1. Introduction

1.1 Aims of the study

The main aim of this project is to describe all of the fossil content that is found within the Downton Bone Bed (DBB) at Weir Quarry and to describe the sedimentology of the section recorded at Weir Quarry including the DBB. This study will be the first to focus solely on the DBB since its original discovery (and naming) more than 110 years ago by Elles and Slater (1906), and will allow for a palaeoenvironmental reconstruction to be produced for the DBB.

To achieve this, fieldwork was conducted to collect samples to be processed so that the fossil (micro and macro) and sedimentology could be investigated. This collection of material was followed by laboratory processing (discussed in the methods chapter) and the extensive use of scanning electron microscopy. Secondary aims for this project are to assess the current state of DBB exposures in the historically significant field area of Ludford and Downton Gorge and to compare the DBB with other known Silurian bonebeds to provide a broader context to the formation and significance of the DBB. To achieve these aims a mixture of fieldwork, visits to research institutes (e.g. NHM, U.K.), the loaning of ex-situ material collected by Elles and Slater for their 1906 paper and literature reviews were carried out.

1.2 Bonebeds: definition and genesis

This section discusses the findings of the book "*Bonebeds: genesis, analysis, and paleobiological significance*" by Rogers et al. (2007) who provide an excellent framework for the definition of bonebeds and their genesis.

Bonebeds are concentration Fossil Lagerstätten consisting of vertebrate skeletal elements (teeth, dermal armour, calcified cartilage and bone). They first appear in Early Palaeozoic strata, notably the Harding Sandstone Formation (Ordovician) of Colorado, U.S.A. (Walcott 1892; Sansom et al. 1995).

1.2.1 What is a bonebed?

The definition of bonebeds has had a long history of discussion (summarised in Table 1.1). The term appears to have first entered the lexicon when Roberts (1842), in reference to the British Rhaetian Bone Bed (RBB) defined it as being "composed of fragments of teeth and bones in an extraordinary manner". His definition did not quantify what a bonebed is, referring only to their rich volume of vertebrate material. Once the term became established, other workers retrospectively renamed established deposits such as the Ludlow fish bed as the Ludlow Bone Bed (Murchison 1852). Despite research on bonebeds continuing through the subsequent 100 years, it appears that little work was carried out on further defining what bonebeds are, which may be due to the fact that other workers at that time felt that the Roberts (1842) definition did the job of defining bonebeds satisfactorily. This lack of study could have been for various reasons. During this time, two world wars took place; this certainly would have curtailed research in Europe. Despite this, at least one paper did discuss bonebeds.

The paper (Reynolds 1928) is concerned with breccias, and in classifying them, they use the term "bone-bed Breccia" to describe bonebeds such as the Rhaetian Bone Bed of Aust Cliff and those in the Wealden of Sussex (Reynolds 1928 and Maidment et al. 2017). Challinor (1967) felt that bonebeds should be defined as "a bed of rock, composed of fossil bones, teeth etc. of vertebrates". Later, Reif (1976) defined bonebeds as; "sediments which are enriched in highly fractured and abraded vertebrate bones", or noted it as "A term applied to several thin strata or layers containing innumerable fragments of fossil bones, scales, teeth, coprolites and other organic debris". He continued "Bonebeds appear abruptly in sections which are otherwise poor in vertebrate remains; as a rule, they have high lateral persistence (up to 50,000 km^2 [*sic*]) and a thickness of several mm to 20 cm, often they form series of 2 to 20 layers within one section".

Antia (1979b) worked on a definition of bonebeds since previous workers did not state how much vertebrate material is required to label a deposit a bonebed. He added that further confusion was caused by the interchangeable use of the term bonebed and fish bed which Howell (1957) felt were synonymous. Antia also felt that Reif's (1976) definition was not valid as he had stated, "As a rule, they have high lateral persistence (up to 50,000 km^2)". Antia noted that some bonebeds are known only

from their type localities and used the Temeside Bone Bed (TBB) (wrongly) and DBB as examples. Antia (1979b), however, did suggest that even if a vertebrate deposit occurs in a restricted geographical area, it can still be regarded as a bonebed. Antia (1979b) also proposed that "the term bonebed should not be applied to zones or layers of bonebed material but only to a single layer of vertebrate rich sediment" and that "a group of bonebeds should be called bone-bed facies". At the base of the Downton Castle Sandstone Formation within the Ludlow Bone Bed Member there is the main bonebed at the base of the member, but there are numerous thinner bonebeds above it, and thus here the term bone-bed facies is appropriate. Antia (1979b) continued to attempt to define bonebeds by focusing on their mineralogical content by reviewing at the studies of Sykes (1977) and Reif (1969) who studied a range of bonebeds and considered their overall phosphatic content. Antia (1979b) suggested that a revised definition for a bonebed could be based on the percentage of phosphate present in a sample of a vertebrate-bearing deposit, stating, "A deposit that contained at least 4.5% phosphate could be considered a bonebed". If accepting the use of calculated phosphate values, then Antia (1979b) suggests that bonebeds can be phosphorites containing apatite as a dominant constituent. However, a reliance on the percentage of phosphate in a bed as defining its 'status' as a bone bed can be problematic. This issue can be illustrated by comparing the DBB, LBB and the Triassic RBB. The DBB, from its first description, was regarded as 'slightly bony' in places (Elles and Slater 1906, p. 210). This diffuse nature would give a lower phosphate percentage when compared to the LBB, which is a condensed deposit. In the DBB or the LBB, the average size of the vertebrate grains is far smaller than is seen in the RBB. The average size fraction used in the study of the DBB is between 500 μm and 212 μm while in the RBB the average size is ≥ 2.4mm (Allard et al. 2015).

The inference here is that due to the more substantial phosphatic content in the larger fragments that this could skew the total percentage of phosphate within the bed. Additionally, the biology of the organisms comprising a Silurian bonebed vs a Mesozoic or Cenozoic bonebed may affect the PO_4 content. In the Silurian, the majority of the vertebrates had cartilaginous endoskeletons, particularly thelodonts and acanthodians (Long 2011). Thus, the only source of phosphate is from the dermal denticles and fin spines. In Late Palaeozoic and younger bone beds, however, although cartilaginous fish (sharks and rays) are still present, Osteichthyes (bony

fish) become more prevalent, and they possess bony endoskeletons. In the Mesozoic many actinopterygians possessed thick ganoid scales which are often dominant components of bone beds. Such mineralised skeletal components increase the potential phosphate content. It is unclear if Antia (1979b) included the phosphate content of coprolites and phosphatic lingulate brachiopods in his analysis; the inclusion or exclusion from deposits might have an impact on the percentage of PO_4 and therefore how the bed is classified.

Following Antia's work on bone beds (Antia 1978, 1979, 1981) there is a gap in bonebed research, although there is a considerable body of work on the formation of fossil concentrations (e.g. Kidwell 1986; Kidwell et al. 1986). However, it was not until the 1990s that Behrensmeyer (1991) defined a bonebed as being "a single sedimentary stratum with a bone concentration that is unusually dense (often but not necessarily exceeding 5% bone by volume), relative to adjacent lateral and vertical deposits". This definition appears to be functional and is that used herein.

Author	Definition
Roberts (1842)	"Composed of fragments of teeth and bones in an extraordinary manner".
Page (1859)	"A term applied to several thin strata or layers containing innumerable fragments of fossil bones, scales, teeth, coprolites and other organic debris".
Challinor (1967)	"A bed of rock composed of fossil bones, teeth etc., of vertebrates".
Reif (1976)	"Sediments which are enriched in highly fractured and abraded vertebrate bones. Very often, the bone fraction is well sorted with grain sizes of fine to coarse gravel. Bonebeds appear abruptly in sections which are otherwise poor in vertebrate remains; as a rule, they have high lateral persistence (up to 50,000 km^2) and a thickness of several mm to 20 cm, often they form series of 2 to 20 layers within one section".
Antia (1979b)	"A deposit that contained at least 4.5% phosphate could be considered a bonebed".
Behrensmeyer (1991)	"A single sedimentary stratum with a bone concentration that is unusually dense (often but not necessarily exceeding 5% bone by volume), relative to adjacent lateral and vertical deposits".

Table 1.1 List of published general definitions of the term "bonebed".

1.2.2 Types of bonebed

Bonebeds have been classified in different ways, focusing on either the size of the vertebrate grains or on their taxonomic diversity.

The first method of classification is based on the size of the vertebrate bioclasts present in the bonebed. According to Eberth et al. (2007), a macrofossil bone bed is "a concentrated deposit of skeletal elements from two or more animals in which most bioclasts (>75%, be they isolated elements or entire skeletons) are >5 cm in maximum dimension". Macrofossil bonebeds are found from the Devonian onwards. Although there are examples of larger vertebrates appearing in the upper Silurian of China (Choo et al. 2014, 2017), these are not preserved in bonebeds. Perhaps the best examples of terrestrial facies macrofossil bonebeds are the mass dinosaur deposits of the Jurassic and Cretaceous (Hatcher 1901; Brown 1935; Sternberg 1970; Lawton 1977; Hunt 1986; Rogers 1990; Varricchio 1995; Ryan et al. 2001; Gates 2005; Mathews et al. 2009; Fiorillo et al. 2010 Maidment et al. 2017; Perales-Gogenola et al. 2019) and the Cenozoic large mammal mass mortality horizons (Peterson 1906; Matthew 1923; Voorhies 1981, 1985, 1992). Macrofossil bonebeds are also known to preserve aquatic and semi-aquatic taxa such as the amphibian-dominated assemblages from the Permian of Texas and Oklahoma (Case 1935; Dalquest and Mamay 1963; Sander 1987), the Carboniferous-Permian boundary of Utah, U.S.A. (Huttenlocker et al. 2018) and the Upper Triassic of India (Mukeriee and Ray 2012). Far rarer in the fossil record are marine macrofossil bonebeds, despite the rich fossil record that they preserve (Martill 1985; Esperante et al. 2008; Bianucci et al. 2016).

Microfossil bonebeds are defined by Eberth et al. (2007) as "relative concentrations of fossils where most component elements (>75%) are ≤ 5cm in maximum dimension". Previously, microfossil bonebeds had been interpreted as containing the abundant remains of animals that were of a body mass no greater than 5 kg (Behrensmeyer 1991). This, however, is seldom the case as microfossil bonebeds can include elements of smaller animals but also skeletal fragments of larger animals (e.g. sharks, dinosaurs and crocodiles) or even whole animals. Eberth et al. (2007) added further to their definition by stating, "They should occur in a stratigraphically limited sedimentary unit and, they should demonstrably contain the remains of at

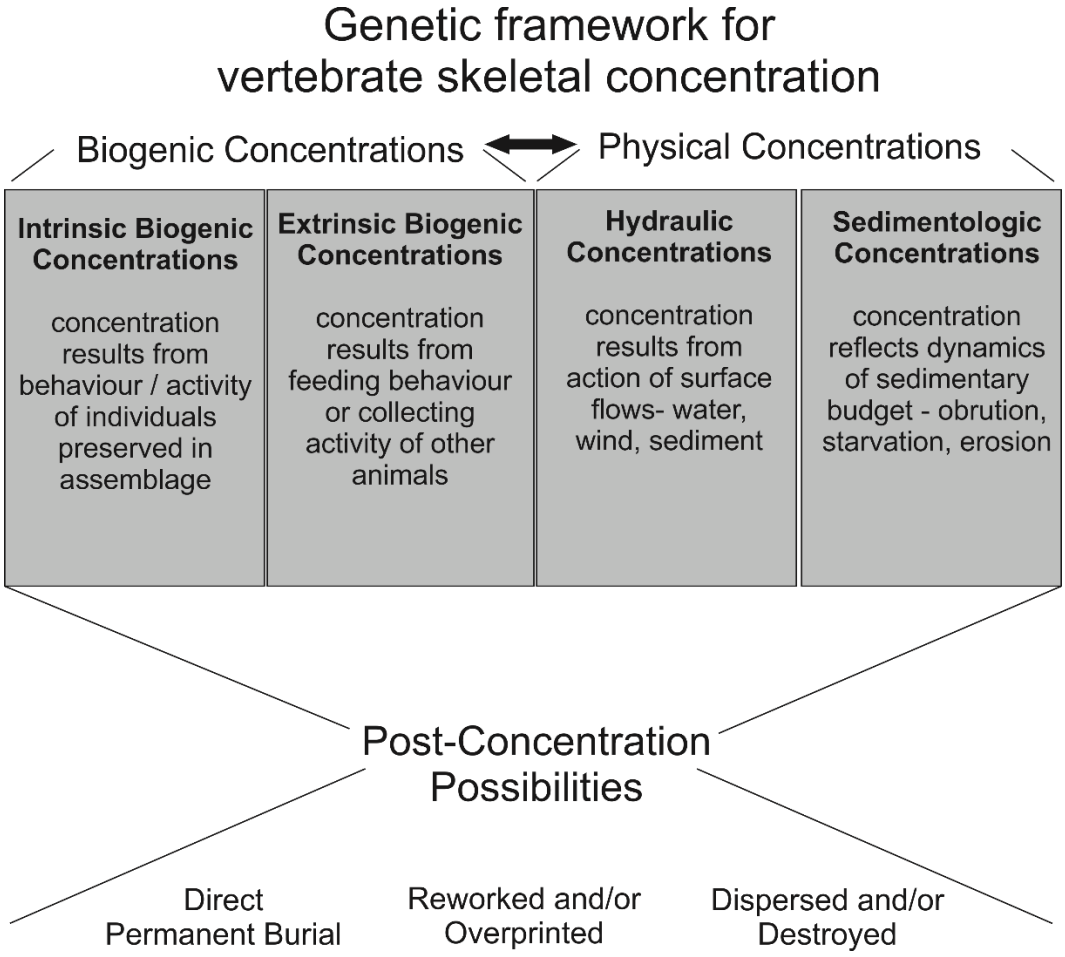
least two individuals". This would allow this definition to work alongside their functional definition of a bonebed. Microfossil bonebeds occur from the Ordovician onwards throughout the Phanerozoic. The oldest bonebed recorded is a microfossil bonebed in the Ordovician Harding Sandstone of Colorado (Walcott 1892; Sansom et al. 1996). Microfossil bone beds are reported from terrestrial and marine facies. Such deposits include the Upper Triassic bonebed of the Marayes-El Carrizal Basin, Argentina (Colombi et al. 2015), the bonebed from the Upper Cretaceous Judith River Formation of Montana (Rogers and Brady 2010), the bonebed of the Upper Cretaceous Maevarano Formation, northwestern Madagascar (Rogers et al. 2013) and the Upper Triassic Rhaetian bone bed of the South West of England (Slater et al. 2016).

An additional bone bed type is bone sands, which consist of sand-sized grains (0.0625-2mm) to granules (2-4mm) of bone, teeth and denticles. The vertebrate elements are often highly abraded with high degrees of sphericity, and are often so poorly preserved that they cannot be identified, only placed within higher taxonomic groups, although occasionally more intact skeletal elements can also be found (Burrow and Turner 2012). Bone sands can vary in geometry from localised lenses to widespread, but usually thin sheets, associated with unconformities, like the bone sands of the Muschelkalk/Keuper Bone-Beds (Middle Triassic, SW-Germany) (Reif 1982).

Bonebeds may also be classified according to their taxonomic content and diversity. There are three groups, discussed by Behrensmeyer (2007), modified from Rogers and Kidwell (2000). Monotaxic bonebeds are composed of multiple elements of two or more individuals of the same species. Paucitaxic bonebeds are comprised of multiple elements from two or three different species. Multitaxic bonebeds consist of skeletal remains from multiple species.

1.2.3 Conceptual models of bonebed genesis

To understand the genesis of bonebeds, it is essential to understand how concentrations of skeletal grains can form. This subject has been discussed thoroughly (Weigelt 1927, 1989; Brongersma-Sanders 1957; Schäfer 1962, 1972; Behrensmeyer and Hill 1988; Shipman 1981; Behrensmeyer 1991, 1992, 2000; Martill 1991; Lyman 1994; Kidwell 2013; Tomašových et al. 2016). Rogers and Kidwell (2007) considered two main categories of vertebrate concentration origins: biogenic and physical (Text-fig. 1.1).



Text figure 1.1 The different processes that lead to the formation of bone beds (modified from Rogers and Kidwell 2007).

1.2.4 Biogenic concentrations

Concentrations of biogenic origin are divided into two subcategories: intrinsic and extrinsic. Intrinsic biogenic concentrations result from the behaviour and activity of organisms that lead to organisms being preserved in concentrated death assemblages. An example of the behaviour or activities that can result in this is natal philopatry (spawning behaviour in fish). Some can operate in concert with environmental factors such as drought during which time animals congregate around water sources resulting in a concentration of vertebrate remains (Shipman 1975; Haynes 1988, 1993; Rogers 1990; Dudley et al. 2001). Therefore, the "mechanism" in forming concentrations of vertebrates under intrinsic biogenic conditions is the hard part of producers themselves (Gates 2005; Mihlbachler et al. 2018).
Extrinsic biogenic concentrations are caused by other organisms forming accumulations of vertebrate hard parts such as the bone-rich faecal masses (from e.g. Hyaenidae) and regurgitates (e.g. from Strigiformes [owls]) (Mayhew 1977; Dodson and Wexlar 1979; Hoffman 1988; Kusmer, 1990; Schmitt and Juell 1994; Laudet and Selva 2005). However, it is not only predatory animals that can form extrinsic concentrations: rodents, such as porcupines and packrats, have a propensity to collect bones (e.g., Brain 1980, 1983; Shipman 1981; Betancourt et al. 1990).

1.2.5 Physical concentrations

Physical concentrations are the other main type of bonebeds. This category is subdivided firstly into hydraulic concentrations resulting from the interaction of surface flows such as water, wind and sediment, and secondly into sedimentological concentrations reflecting the sedimentary dynamics, such as obrution, starvation and erosion.
There is significant overlap between sedimentological concentrations and hydraulic concentrations as similar processes (waves, currents, etc.) control sediment movement; however, sedimentological controls focus on the non-bioclastic sedimentary budget. This can be in three forms: positive (whereby sediment is added to the system), negative (caused by erosion and degradation which would include dissolution), and zero (starvation, dynamic or total bypassing) (Rogers and Kidwell 2007).

Post-concentration events may also affect the nature of the final bonebed deposit: burial, reworking and finally dispersal. When considering physical processes for concentrating vertebrate remains, it is sensible to consider the vertebrate remains as sediment grains (bioclasts). This is particularly relevant in relation to microvertebrate bone beds as due to their small size; they are easier to conceptualise as sediment grains (Martill 1991).

1.2.5.1 Hydraulic concentrations

The behaviour of vertebrate bioclasts in fluid flows is dependent upon their grain size, shape and density (Rogers and Kidwell 2007). The potential for accumulations of vertebrate hard-parts to amass because of physical hydraulic processes is dependent on various factors, such as the persistence of the hydraulic medium, the threshold velocity of bioclasts relative to that of the inorganic matrix, as well as the abundance of bioclastic material delivered to the system (Rogers and Kidwell 2007; Cavin et al. 2010). Two important mechanisms of hydraulic concentrations are: fluvial hydraulic accumulations and strandline hydraulic accumulations. Behrensmeyer (1988) studied vertebrate preservation in fluvial settings and recognised assemblages that accumulated under the influence of "sustained and active flow resulting in channel-lag assemblages". These channel lag assemblages are generally considered parautochthonous to allochthonous. If a channel is abandoned, then it will result in a channel fill assemblage (Rogers and Kidwell 2007).

Considering vertebrate hard parts as grains, they may exhibit some taphonomic features that are evidence of various biological and physical processes occuring both before and during their interactions with fluvial processes. These features could include abrasion, indicating sustained interaction with abrasive sediment driven by currents; caution must be taken though as some hard parts like teeth can show abrasion that took place in life (tooth to tooth occlusal wear facets for example). Some grains can also appear fresh and angular (Behrensmeyer 1982, 1987, 1988) this might indicate a range of taphonomic processes having taken place.

Currents often result in size and shape sorting of grains as well as generating a preferred orientation within a prevailing current (Voorhies 1969; Behrensmeyer 1975; Korth 1979; Shipman 1981). In fluvial settings, vertebrate articulation is generally low and this is especially the case in microfossil bonebeds (Rogers and Kidwell, 2000).

The transport of vertebrate bioclasts and their subsequent dispersal has been studied to a larger degree (Dodson 1971; Wolff 1973; Lawton 1977; Badgely 1986; Behrensmeyer 1988; Hook and Fern 1988). Some workers undertook experimental studies using different vertebrate groups. Dodson (1973) experimented in flume tanks using disarticulated microvertebrate elements from mice and amphibians) Behrensmeyer (1975) studied the influence of bone size, shape and density on transport potential, using mammals, looking at the theoretical considerations of dispersal. She experimented on bone settling velocities and, from this, was able to estimate the hydraulic equivalence of modern and fossil bones and their associated sedimentary matrix. Behrensmeyer (1975) also looked at channel geometry, flow regime, and burial potential as all will have an impact on bone transport, dispersal and accumulation. Blob (1997) looked at non-mammalian elements; the analogue he chose for the study was the spiny soft-shelled turtle (*Apalone spinifera*). It was found that the turtle elements fell into three groups of dispersal, which formed in a reasonably predictable fashion (Text-fig. 1.2).

Early Dispersal	Intermediate Dispersal	Late Dispersal	Variable Dispersal
Atlas (1)	Hyoplastron (9)	Metatarsal (IV) (34)	Skull (E/I) (o) (3, 8, 12, 13, 27)
Sternum (2)	Cervical vertebra (11)	Fibula (36)	Posterior costal (E/I) (o) (6, 10)
Astragalus/calcaneum (4)	Humerus (14)	Xiphiplastron (37)	Nuchal (E/I) (o) (7, 20)
Free rib (5)	Epiplastron (15)	*Dorsal centrum (38)	Anterior costal (I) (o) (18, 22, 28)
	Lower jaw (17)		Pedal ungual phalanx (I) (v) (19)
	Radius/ulna (23)		Hypoplastron (I) (v) (21, 24)
	Entoplastron (25)		Femur (I/L) (o) (31)
	Tibia (26)		Scapulocoracoid (I/L) (v) (33)
	Pedal phalanx (V-2) (29)		*Dorsal centrum (I/L) (v) (16, 35)
	Neural (30)		
	Pelvis (32)		

Text figure 1.2 Table 5 from Blob (1997), demonstrating the consistency of the three groups of turtle elements dispersal patterns with a fourth (variable).

Furthermore, the initial orientations of the turtle elements on the flume bed were found to have a significant effect on their dispersal potential. Due to the fact that threshold velocities for entrainment of turtle elements correlated poorly with bone density, Blob (1997) cautioned against the uncritical application of mammalian hydrodynamic sorting patterns in regards to non-mammalian assemblages. The

dynamics of bone concentration under active flow in modern fluvial channels is not fully understood with regard to bone degradation, such as rounding and abrasion (Rogers and Kidwell 2007). This is unfortunate given how common these deposits are (Lawton 1977; Korth 1979; Behrensmeyer 1987, 1988; Koster 1987; Eberth 1990; Fiorillo 1991; Badgley et al. 1995; Rogers and Kidwell 2000). In some cases, ancient fluvial bone assemblages have been linked to mass-death events, and in this scenario, the concentrations are hypothesised as being parautochthonous deposits sourced from nearby (Voorhies 1969; Eberth and Ryan 1992; Ryan et al. 2001).

Other deposits have been interpreted as attritional accumulations that developed over time as bones and teeth were transported hydraulically within a fluvial system. Two methods of trapping sediment are often used to explain bone accumulations. One is in-channel obstructions caused by large carcasses or trees (Fiorillo 1991; Le Rock 2000). The other is a sudden drop in hydraulic competence, often associated with sinuous channel stretches (Lawton 1977). In such scenarios, the flow of water slows to the point where vertebrate hard-parts drop out of suspension and are no longer entrained, stop rolling or stop saltation (the last being of particular importance for microfossils). Aslan and Behrensmeyer (1996) noted that even after many years, some bones and teeth travelled only 100 m or so within a channel. This suggests that these types of deposits would take a long time to form and are being at least in part sourced from pre-existing concentrations (Eberth 1990). This could account for the mix in taphonomic grades often found in bonebeds (Rogers and Kidwell 2007).

The other type of hydraulic concentration is a strandline hydraulic accumulation, which develops due to wave action. Vertebrate hard parts are often derived from floating carcasses, which become anchored in the swash zone allowing the carcass to be disarticulated by wave and scavenger activity. The action of onshore and longshore transport can also act to transport material along a strandline, and further concentrate it. Skeletal components in strandline deposits can be orientated tangentially to the shoreline or, in the case of irregular elements where part of the element acts as a pivot, perpendicular to the shoreline. Vertebrate remains along strandlines are associated commonly with plant debris particularly on the margins of freshwater bodies.

An example is documented in Smithers Lake, Texas (a “recent” mass mortality event) (Weigelt 1927 and 1989). At Smithers Lake, vertebrate carcasses accumulated alongside large amounts of plant debris during intense winter storms. A multi-individual accumulation of skeletal debris along a strandline is suggestive of event-heightened mortality. This has been tested by comparing a recent lake deposits of disarticulated bird elements (pelicans and cormorants) that had died previously from infectious disease to an Eocene accumulation of *Prebyornis*. Leggitt and Buchheim (1997) noted the similarities both had in their taphonomic character and the strong alignment of the elongate elements (humerus, radius, ulna, tibiotarsus and tarsometatarsus) in relation to the shorelines.
Rogers et al. (2001) studied a Triassic deposit in Argentina of partially articulated tetrapods, which was suspected to be a strandline deposit. The reasons for this were because the deposit shows key features such as distribution in a narrow linear swathe, and alignment of skeletal debris, including good examples of parallel-aligned carcasses.

1.2.5.2 Sedimentological concentrations

Probably one of the best settings for the accumulation of vertebrate hard parts is during a non-deposition or sedimentary starvation event. This allows vertebrate hard parts to build up from contemporaneous vertebrate populations (Behrensmeyer and Chapman 1993). Concentrations build up by passive means and the longer the hiatus, the greater the potential for the deposit becoming richer and laterally more persistent. Conversely a lack of sedimentation may result in increased post-mortem destructive processes on or near to the depositional interface so that any ‘advantage’ of the lack of sedimentation in building up accumulations of vertebrate material could be lost due to heightened taphonomic removal (Rogers and Kidwell 2007).

Stratigraphical records of marine settings can contain “time-rich” hiatal concentrations of vertebrate hard parts. Such deposits are often generated during significant hiatuses in sedimentation, such as parasequence-boundary flooding surfaces, transgressive surfaces and mid-cycle surfaces of maximum transgression (Conkin et al. 1976, 1999; Sykes 1977; Kidwell 1989, 1993; Macquaker 1994; Turner et al. 2001; Walsh and Naish 2002; Allulee and Holland 2005).

The formation of these hiatal deposits, can depend upon the conditions present, (e.g. sediment starvation of submarine palaeo-highs, distal portions of basins, and transgressive shelves; sediment bypassing of shallow-water environments; erosional truncation associated with rapid transgression and base level lowering (Kidwell 1991a,b). They can be associated with either scarce or common shelly remains from macrobenthos, and range in condition from articulated specimens (assumed to be associated with anoxia and reduced sedimentation-taking place within a maximum transgression; (Brand et al. 2004). Other deposits consist of greatly comminuted, abraded and polished teeth as well as fragments of bones of marine taxa (produced from the erosional reworking of underlying marine strata). A common factor in these marine hiatal concentrations is that they are thinner than coeval less fossiliferous strata. They also typically bear tangible evidence of extended low net sedimentation, such as ecological condensation and admixtures of hard parts with different taphonomic or diagenetic histories (Rogers and Kidwell 2007). Despite this, within the marine realm, it appears that the production of new elements (vertebrate and macroinvertebrate hard parts) compensates for the destructive forces during a hiatus, such as repeated small-scale burial-exhumation cycles (Kidwell and Behrensmeyer 1988; Rogers and Kidwell 2000). Destructive processes can include trampling, scavenging, chemical weathering, exposure to UV, fungal and microbial attack and freeze-thaw. Destructive soil processes (e.g., wet/dry alteration of oxidation states) can also contribute to the destruction of skeletal elements, as can exhumation-burial cycles (via bedform migration within channels for example). Although there are negative factors that could limit the number of vertebrate concentrations present in a terrestrial system, there are terrestrial settings where accumulations can occur. One such example is palaeosols, where hiatal concentrations are most likely to form because they allow for the build-up of vertebrate hard parts, which in turn relies on long-term landscape stability. This is because it takes a long time for these accumulations to form, as well as there being the need for skeletal input locally exceeding the rate of recycling. An example from the Amboseli Basin of Kenya indicates that even given 10,000 years of attritional input, the density of bone would likely still be as low as less than one bone per square metre (Behrensmeyer 1982).

Terrestrial attritional accumulations can also form in flood basin lakes and ponds, mainly because they represent environments that support diverse vertebrate communities. Being a source of fresh water within an ecosystem, ponds and lakes often are a focus for animal activity (Coram et al. 2017). Animals often die in these settings due to predation, disease and senescence, resulting in a death assemblage developing, the nature of which of course depends upon the vertebrate population and the chemical nature of the water body (as if too acidic, i.e. <7pH, bone will be removed by dissolution). The ideal water chemistry needed to preserve bone and teeth long term is a high pH and low Eh. Finally, the rate of sedimentation, of course, plays an important factor in vertebrate preservation. Perhaps surprisingly, slow sedimentation can play an important part in preservation, allowing skeletal debris to accumulate to sufficient levels to generate a bonebed. This type of bonebed is typically tabular, organic-rich and laterally extensive, and hard skeletal parts are numerous but often disseminated throughout the bone-rich horizons (rather than concentrated in pockets or along with bed contacts) (Sahni 1972; Rogers 1995). The vertebrates are also disarticulated and dissociated so that it is virtually impossible to confirm that any two skeletal elements are from the same individual. Such attritional accumulations, regardless of their sedimentary context, will be time-averaged to a greater or a lesser degree. The longer the duration of the hiatus during which a bonebed forms, the greater the chance for the assemblages becoming ecologically heterogeneous. These terrestrial assemblages are parautochthonous, the material coming from attritional mortality in the vertebrate community. Like so many bonebeds, the preservational quality of bones and teeth is variable due to elements entering the system at different times.

The process of erosion can also have an impact on bone bed formation. Erosional forces can preferentially remove the siliciclastic sedimentary matrix, leaving behind denser lag deposits of skeletal material previously exhumed from older deposits. These vertebrate lag concentrations will likely form in channels within fluvial systems and high-energy shallow marine settings, e.g. shorelines, intertidal and subtidal channels (Wells 1944; Behrensmeyer 1982, 1988; Reif 1982; Smith and Kitching 1997; Rogers and Kidwell 2000). In theory, the deeper the erosion cuts into older sediment or strata, the greater the volume of previously deposited vertebrate material that can be incorporated into a concentrated lag deposit. These erosional

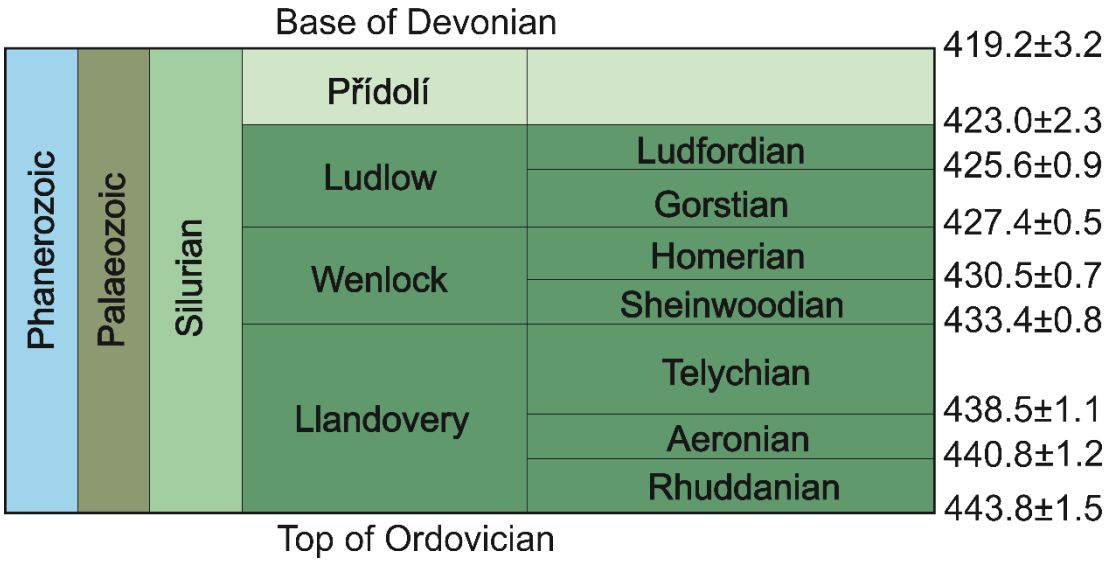
deposits often undergo more multiple reworking events than a bone bed formed under aggradational conditions. This makes erosion another agent of skeletal breakdown and potential transport out of the local system as well as exhumation, which may have a small net positive effect on hard-part supply. Some more resilient hard-parts, like teeth or material that has been permineralized, can potentially endure erosion and accumulate in lag form. While in these lags or other quiet conditions, it has been suggested that mineralization can begin before the material is finally buried. This is the pre-fossilisation described by Reif (1982). Rogers and Kidwell (2000) examined the association between vertebrate skeletal concentrations and erosional surfaces in the Upper Cretaceous Two Medicine and Judith River formations, Montana. They failed to find any clear correlation between the abundance of skeletal material and the inferred duration of the hiatus. The most significant erosional discontinuity in the section was the 80 Mya sequence boundary in the Two Medicine Formation which was almost devoid of any vertebrate skeletal debris whereas, conversely, erosion surfaces of a lesser extent and duration interpreted as marine flooding surfaces, preserved scours inside individual fluvial channels which were often mantled by diverse skeletal concentrations. These concentrations closely tracked the abundance of vertebrate material in underlying and laterally disposed facies. This suggests that the skeletal material originated from local erosional reworking that underwent little subsequent lateral dispersion.

Erosion-generated bonebeds will be time averaged to a variable degree. The extent of time-averaging is dependent on the depth of incision and the age profile of the bioclasts preserved in the underlying and laterally disposed strata. If the scenario is exclusively exhumation, then the resultant lag concentration will be entirely older than the hiatal episode that formed the surface. The taphonomic features seen in exhumation might include abrasion, rounding, polishing (Rogers and Kidwell 2000), angular breakage patterns (Morlan 1984), variable diagenetic signatures (Trueman and Benton 1997) and environmentally mixed assemblages. There are also sedimentological features consistent with exhumation, including stratigraphical evidence of erosional surfaces and exotic sedimentary matrix embedded within or adhering to the exhumed skeletal debris. Some care should be taken with the latter as fine clays and silts that have travelled within the fluvial system can enter the bones, and contrast with the coarse-grained fraction that noticeably is represented in the bed load.

Bonebeds can also form by obrution (Seilacher et al.1985; Brett 1990; Bruton 2001), whereby a concentration of vertebrate hard-parts, often originating from an assemblage of carcasses, is permanently buried by a single and unusual depositional event. Examples of such rapid sedimentation include ash fall, slipface avalanche or slump/bank collapse and catastrophic river flow. This type of concentration is certainly helped by group activity such as communal habitation, herding, and predator-prey interaction. Fossorial animals are particularly susceptible to obrution as sediment can easily block their burrows. There are few examples of obrution of burrowing vertebrates in the fossil record, however. Notable examples include articulated pairs of therapsids preserved within their burrows in the Upper Permian Beaufort Group of the Karoo Basin in South Africa (Smith 1993), lungfish (*Gnathorhiza bothrotreta*) found in aestivation burrows in the Lower Permian of New Mexico USA (Berman 1976), the ornithischian dinosaur (*Oryctodromeus cubicularis*) in the mid-Cretaceous Black Leaf Formation of southwest Montana, USA (Varricchio et al. 2007) and four intact hyena skeletons found in an ancient burrow system from the Pleistocene Olorgesailie Formation of Kenya (Potts et al. 1999). Catastrophic sedimentation events can also bury assemblages of non-gregarious animals (e.g. dinosaurs, lizards and mammals). A classic example of this is the *Oviraptor* sat on its nest, entombed within the structureless sandstones of the Tolgod locality in the Gobi Desert, Mongolia (Norell et al. 1995). An example of gregarious animals being killed by a catastrophic sedimentation event forming a death assemblage is at the Poison Ivy quarry of Nebraska, where many *Teleoceras* (an early rhino) were killed by an ash fall from a pyroclastic flow, during the Miocene (Voorhies 1985, 1992). There is limited evidence of time averaging in these types of unusual sedimentation because it is presumed that the animals died and were buried simultaneously (Finch et al. 1972; Voorhies 1985, 1992). In most circumstances, the assemblage should also be autochthonous, although some events may cause slight transport of carcasses before final burial (Rogers and Kidwell 2007). Both the degree of articulation and element association as well as the preservational quality should be high. However, some diagenetic degradation can occur (Chiappe et al. 1998; Grellet-Tinner 2005). The assemblage should also be within or beneath a thick and/or anomalous sedimentation unit, e.g. ash bed or debris flow deposit. Bonebeds remain a broad field of study, and as has been demonstrated there is a range not only of definitions but also methods of formation.

1.3 The Welsh Borderlands during the Silurian

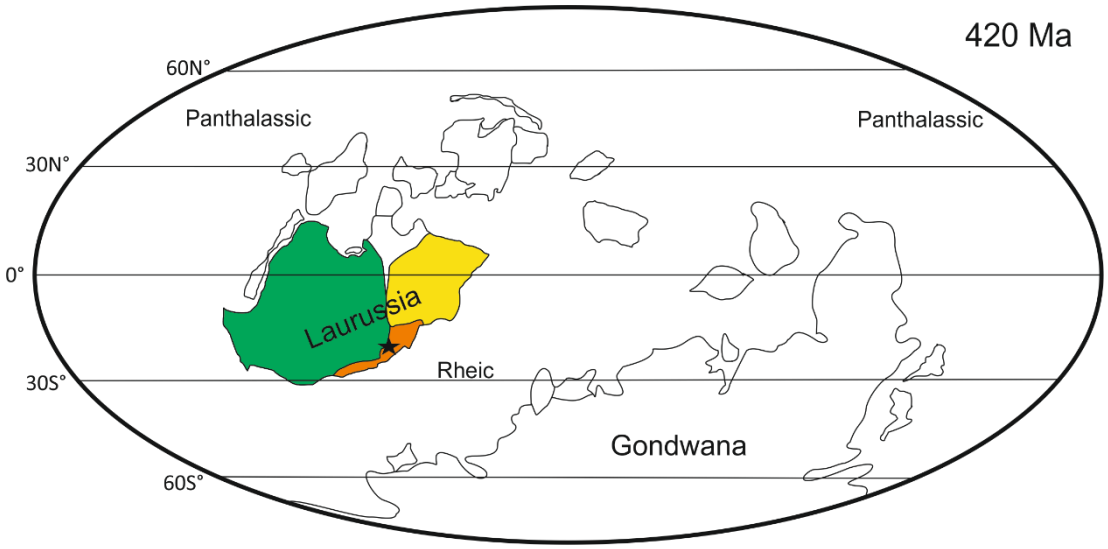
The Silurian is dated to 443.8 ± 1.4 Ma to 419.2 ± 3.2 Ma, however a recent study has placed the start of the Silurian to 442 Ma (Ling et al. 2019) this date was obtained using U-Pb dating. The majority of the Silurian is constrained by the use of Global Boundary Stratotype Section and Point (GSSP's) (Ogg et al. 2016) (Text-fig. 1.3). The Silurian was first a recognised as a division of the rock record by Sir Roderick Impey Murchison (1839) for a distinct unit of rocks from the Welsh Borders of the United Kingdom, and was named after a Celtic tribe, the Silures, who lived during the Iron Age in what is now Wales. It is divided into four series/epochs: the Llandovery, Wenlock, Ludlow and Přídolí. During the Silurian, the area of continental crust that would one day become the U.K. was situated south of the equator (Text-fig. 1.4) (Torsvik and Cocks 2013) on the microcontinent Avalonia.



Text figure 1.3 Chronostratigraphic chart of the Silurian (Modified from Cohen et al. 2013 updated http://stratigraphy.org/index.php/ics-chart-timescale).

The Silurian Period was one of the shortest in the Phanerozoic (*c.* 25 My). The end of the previous period, the Ordovician, was dominated by glaciation and an associated glacioeustatic sea-level low-stand (Brenchley et al. 1994). This situation reversed during the early Silurian with the ice cap located over the South Pole (in what is now North Africa) melting rapidly, and resulting in a worldwide marine transgression (Fortey 1984). During the Silurian, there were subsequent fluctuations in sea level believed to be due to changes in the volumes of ice at the poles (Loydell

1998, 2007: Díaz-Martínez and Grahn 2007; Finnegan et al. 2011). There was also tectonic activity resulting from the closure of the Iapetus Ocean (McKerrow et al. 2000; McConnell et al. 2019). The Silurian was regarded for many years as being largely a period of comparative climatic stability with a warm climate. This view has changed dramatically in recent years, due to the identification of four major positive carbon isotope ($\delta^{13}C_{carb}$) excursions during the Silurian Period (Loydell 2007; Calner 2008), indicating that fundamental changes in the global carbon cycle occured. With four excursions of >+4‰ in a period of only 25 million years, these are more frequent than at any other time in the Phanerozoic (Cramer and Saltzman 2005).

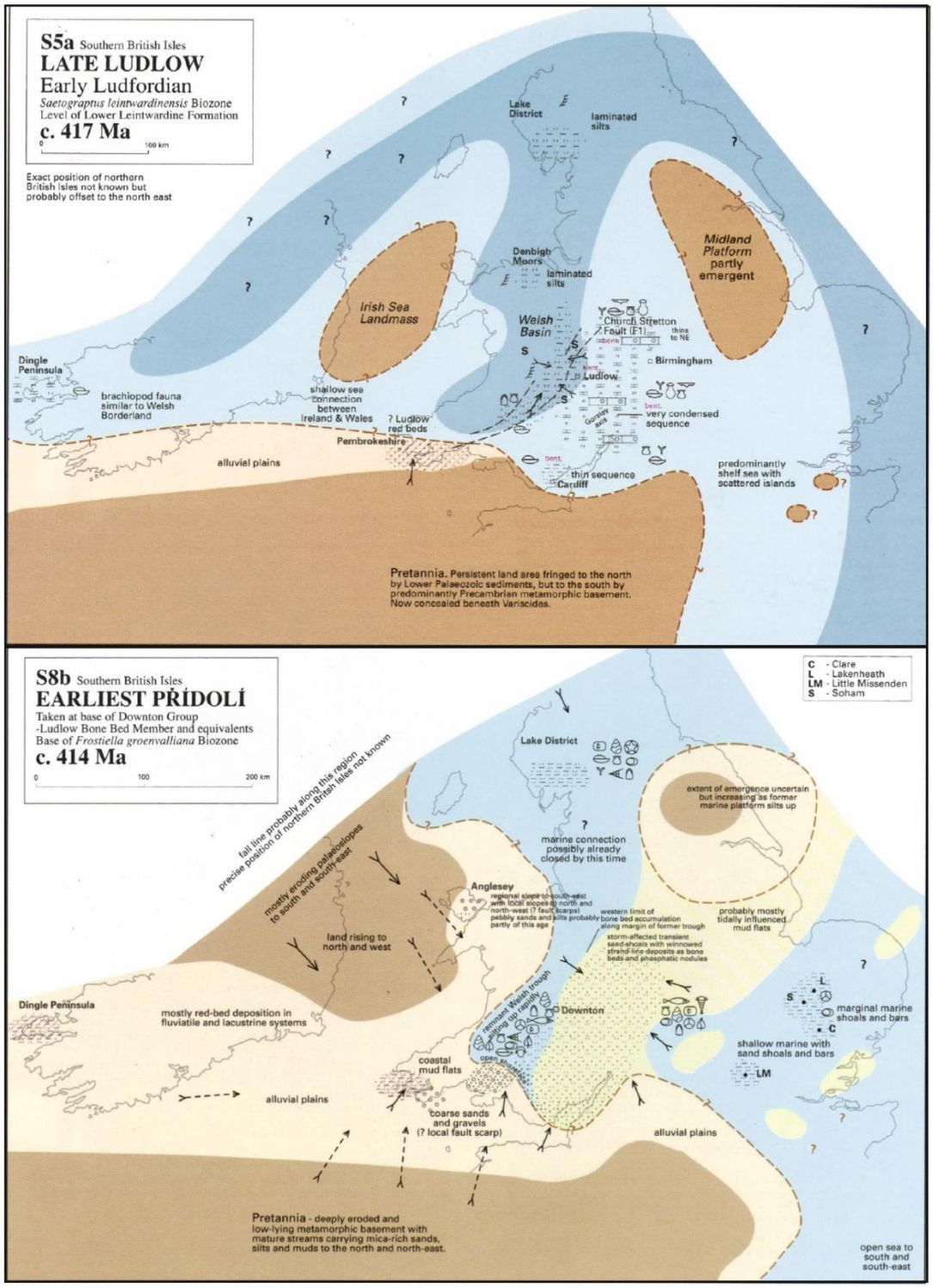


Text figure 1.4 Palaeocontinental reconstruction for the Ludfordian (modified from Torsvik and Cocks 2013), with the main continents making up the supercontinent of Laurussia being Laurentia (green), Baltica (yellow) and Avalonia (orange). Star shows the position of the Welsh borders.

The Llandovery Epoch was characterized by marine transgressions early on, which were largely eustatic with factors controlling sea level being climatic and tectonic, operating either in tandem or in opposition. The Wenlock Epoch is typified by the expansion of shallow seas and the widespread deposition of carbonates. In the Welsh Borderlands, this led to the deposition of the Woolhope Limestone and Much Wenlock Limestone formations. The Ludlow Epoch marked the start of the dominance overall of marine regression (Text-fig. 1.5). This led to restricted marine and fluvial conditions which became common late in the epoch and to the Welsh and Lake District basins becoming silted up and much shallower. Before the end of the

Ludlow, terrestrial red beds developed in Pembrokeshire and South West Ireland (Bassett et al. 1992).

The Přídolí Epoch was a time of expansion of terrestrial sediment deposition across the British Isles, leading to the dominant establishment of non-marine depositional regimes (Text-fig. 1.5). Only the south-easternmost part of England remained fully open to marine influences while the Welsh Borderlands-Midland Platform was susceptible to short-lived, periodic flooding by the marginal sea until well into the Přídolí (Bassett et al. 1992).



Text figure 1.5 The southern British Isles during the late Ludlow and Přídolí epochs straddling the time when the DBB was deposited: dark brown = Hilly terrain, buff = Alluvial plains, dark blue = Deep seas and light blue = Shallow seas (from Ingham et al. 1992).

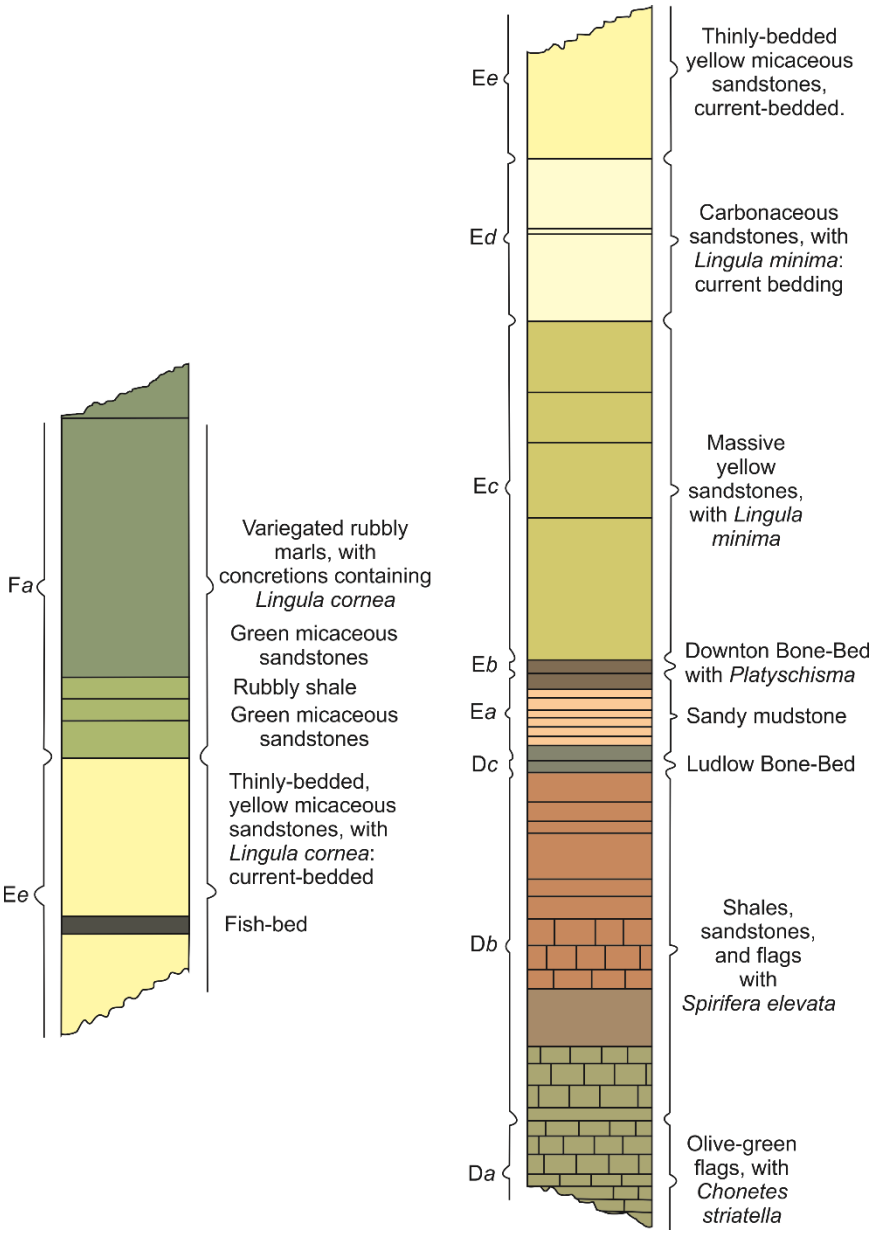
1.4 The Downton Bone Bed

This thesis focuses mainly on a bonebed exposed at Weir Quarry, Herefordshire. It is within the Platyschisma Shale Member of the Downton Castle Sandstone Formation. This is identified herein as the Downton Bone Bed (DBB) of Elles and Slater (1906) for the reasons outlined below.

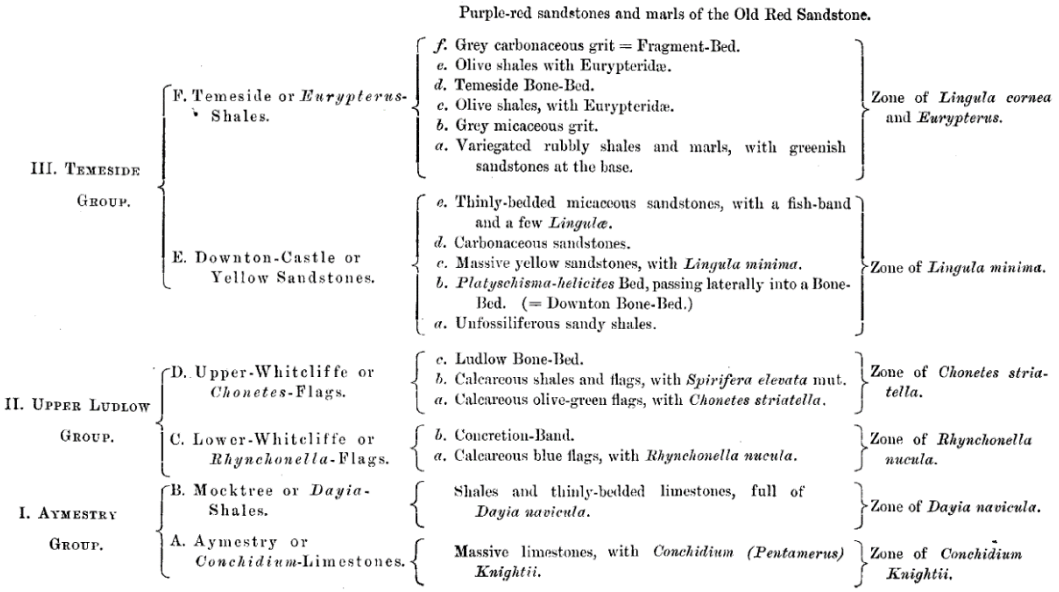
1.4.1 Stratigraphical position of the Downton Bone Bed

Elles and Slater (1906) identified the "Downton Bone-Bed" within their unit E*b* (Text-fig. 1.6), noting that it passes laterally from their "*Platyschisma-helicites* Bed" (Text-fig. 1.7). Although unit E*b* was recorded at several locations in the Ludlow area by Elles and Slater (1906), only in sections near to Downton Castle and within the Downton Castle inlier, approximately 5 km W of Ludlow, was a bonebed recorded within it. At the most famous LBB locality, Ludford Lane, just south of Ludlow, no bone bed was recorded by them within unit E*b*.

Elles and Slater's (1906) unit E*b* is now referred to as the Platyschisma Shale Member, which is ≤ 2 m thick (Bassett et al. 1982). This is well exposed at Weir Quarry where logging of the section within the quarry revealed only one well-developed bonebed. On the basis that Elles and Slater's (1906) extensive fieldwork in the area revealed only the one bonebed within their unit E*b*, it seems certain that the bone bed studied herein must be the DBB.



Text figure 1.6 Reproduction with modifications of figure 6 from Elles and Slater (1906) showing the Downton Bone-Bed in the section at Forge Bridge (SO 45396 74989) scale on original is 6 feet to the inch.



Text figure 1.7 Nomenclature of stratigraphy established by Elles and Slater (1906), taken from an unnumbered figure on p. 198.

1.4.2 Other studies of the Downton Bone Bed at Weir Quarry

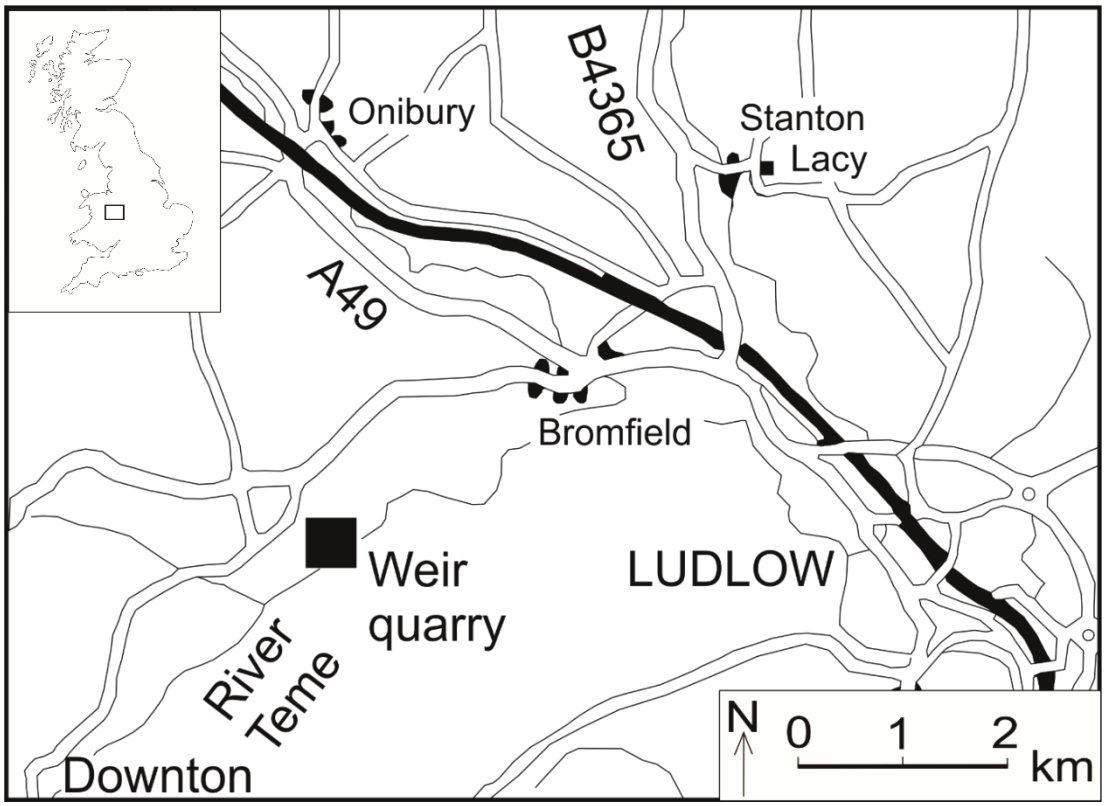
The DBB was recorded at Weir Quarry by Whitaker (1962, p. 338), where it is described as being well exposed, and by Dineley (1999, p. 102, in which the locality is referred to as Forge Rough Weir) where it is noted that there is "a fine exposure of the Ludlow Bone Bed, the Downton Castle Sandstone Formation and a discrete Downton Bone Bed." Extensive examination of the strata exposed in Weir Quarry by D. Loydell, A. Butcher and R. Loveridge (while also collecting samples from trackside exposures at the quarry entrance for the isotope analyses presented in Loydell and Frýda 2011), together with fieldwork within the quarry revealed only one well-developed bonebed within the Platyschisma Shale Member. Again, it seems that this must be the DBB. A list of known and published DBB localities is provided in Table 1.2.

Site	Paper cited (if applicable)	Page No.	Grid ref (if avalible)
Forge Bridge	Elles and Slater 1906	210	SO 4548 7501
Downton Castle Bridge	Elles and Slater 1906	209	SO 4447 7427
Forge Cottage	Elles and Slater 1906	210	SO 4533 7503
Ludford Lane	Elles and Slater 1906	210	SO 5118 7412
Linley Brook	Roberts and Randall 1863 & Stamp 1923	230 & 369	SO 6839 9801
Weir Quarry/ Forge Rough Weir	Whitaker 1963	338	SO 4561 7524
Downton Gorge (locality 57)	Holland 1963	163	SO 4449 7427
Downton Gorge (locality 58)	Holland 1963	163	SO 4442 7402
Burrington (locality 136)	Holland 1963	165	SO 4557 7403
Burrington (locality 137)	Holland 1963	165	SO 4575 7406
Lye, Worcester	Turner 1973 appendix	3	SO 929 845
Little Missenden, Buckinghamshire	Turner 1973 appendix	5	SU 920 980
Lye, Worcester, The Hayes	Turner 1973 appendix	5	SO 929 845
Saltwells Quarry near Netherton, Staffordshire	Turner 1973 appendix	5	SO 9335 8708
Elish Barn, SW Corfton Hall	Turner 1973 appendix	5	SO 4356 8435
Lucton Lane, Lucton	Forey 1987	27	SO 4350 6441
Linley Brook	Bradfield and Tucker 1986	378	SO 6868 9817
Track south of Downton Castle Bridge, Shropshire	Miller 1995a	345	SO 4442 7402
Weir Quarry/ New Forge Rough Weir	Dineley and Metcalf 1999	102	SO 456 752
Track south of Downton Castle Bridge, Shropshire	Märss and Miller 2004	1262	SO 4442 7402
Weir Quarry/ Forge Rough Weir	Hauser 2015	62	SO 4560 7525

Table 1.2 List of Downton Bone Bed localities.

1.4.3 The Downton Bone Bed of Weir Quarry

The DBB was studied at Weir Quarry (SO 45617 75208), a disused quarry, located 7.24 km west of Ludlow, Shropshire, UK (Text-fig. 1.8). The age of the bone bed is discussed in subsequent chapters. It is currently considered to be dated *c.* 424 Ma having been deposited during the mid-Ludfordian Age of the Ludlow Epoch (Loydell and Frýda 2011).



Text figure 1.8 Map locating Weir quarry in relation to Ludlow (Modified from Loydell and Frýda 2011).

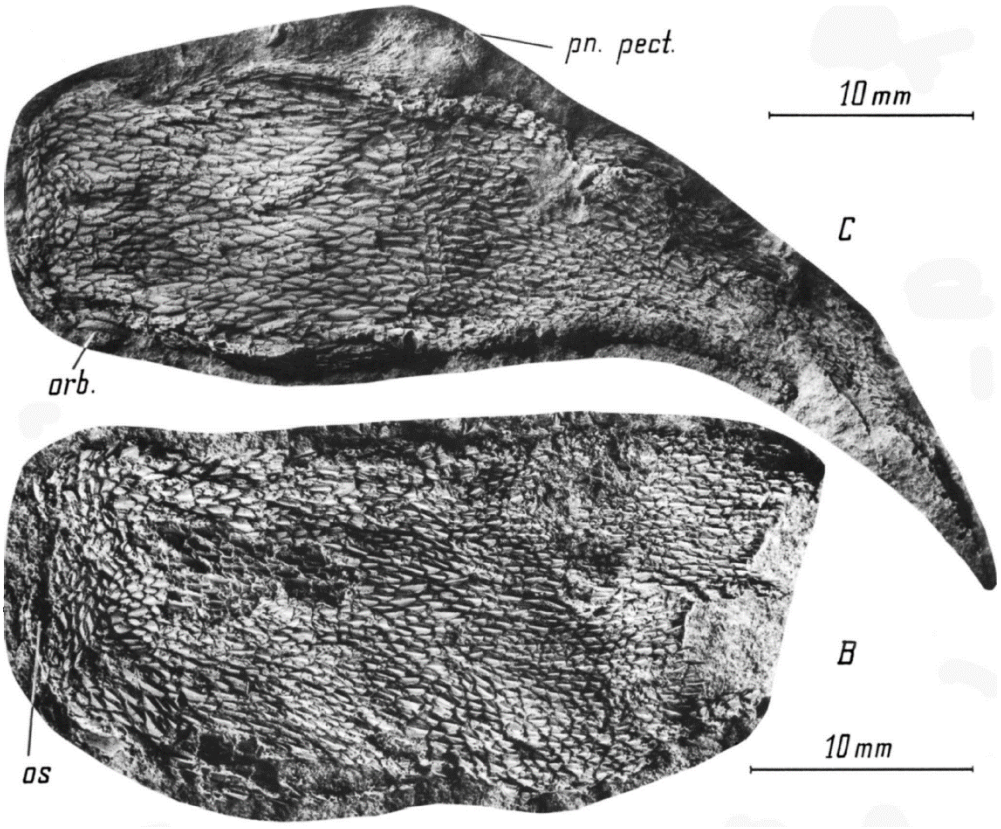
1.5 Introduction to the vertebrates of the Downton Bone Bed.

This section introduces the most common groups of fossil vertebrates in the DBB at Weir Quarry. Compared to much of the Silurian of the U.K., the Downton Castle Sandstone Formation contains abundant vertebrate fossils. It contains two of the three known UK Silurian bonebeds, the LBB and the DBB.

1.5.1 The Thelodonti

The most common type of vertebrate fossil in the DBB is the isolated denticles of jawless fish (Agnatha) known as thelodonts. The Thelodonti is a monophyletic group of fish known from the Upper Ordovician to the Upper Devonian, with a global distribution (Märss et al. 2007). They generally had a small body size, ranging from 7 cm to 60 cm in length (Märss et al. 2007). Thelodonts lived in a wide range of habitats from fresh water, brackish water, shallow-water lagoons and seas, open shelf

and deep-water basins (Märss et al. 2007; Ferrón et al 2018). There are three orders of thelodonts: Archipelepidiformes, Thelodontiformes and Furcacaudiformes. There are taxa based upon both articulated specimens, such as *Phlebolepis elegans* (Pander, 1856) (Text-fig. 1.9), and scale taxa such as *Paralogania ludlowiensis* (Gross, 1967).



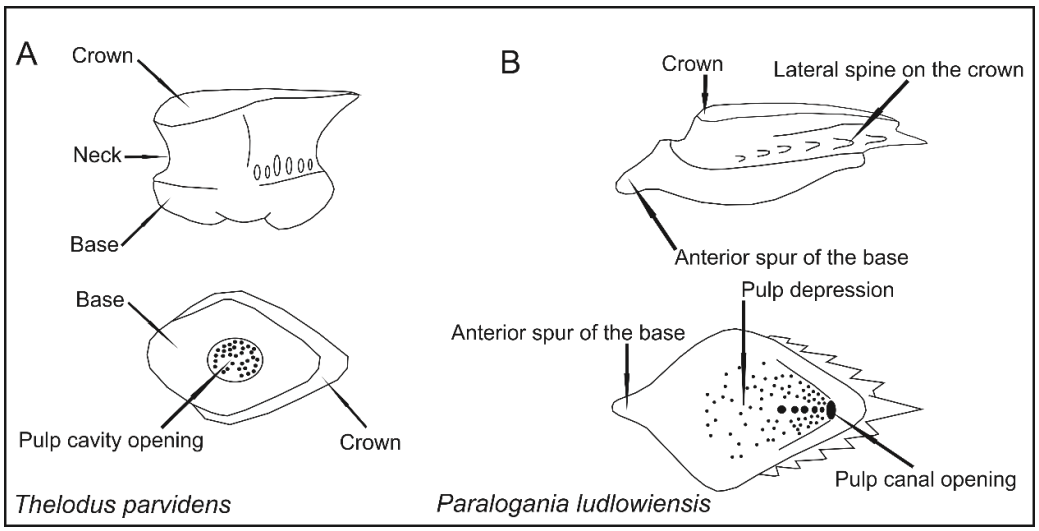
Text figure 1.9 Squamation of *Phlebolepis elegans* (Pander) casts of specimens from Himmiste-Kuigu quarry, Estonia, (Ludlow, Paadla Stage, Himmiste Beds); B, Pi-7050, anterior part of the body with mouth C, Pi-6686, dorsal view showing orbital plates and pectoral fin. Abbreviations: orb. = orbit; os = mouth; pn. pect. = pectoral fin (From Märss 1986).

They had an endoskeleton of cartilage with the impressions of this being preserved in specimens like *Turinia pagei* as well as other soft tissues (pharynx, gill openings, stomach and caudal extremity of the digestive tract) (Donoghue and Smith 2001). The most common thelodont elements found are the scales (Text-fig. 1.10) that made up the squamation over their body; some estimates suggest that they may have had up to 20,000 denticles (Märss et al. 2007). These have been intensely studied over the years. Histologically their denticles are more akin to our teeth than to true bone,

with a pulp cavity and dentine tubules. Their denticles vary in morphology across their bodies. The morphology of the denticles, which in some taxa is ornate, appears to have served primarily as an aid to hydrodynamics with a secondary function of parasite/abrasion resistance and defence (Märss 1986; Märss et al. 2007; Fletcher et al. 2014; Ferrón and Botella 2017). The denticles are classified as head, trunk, transitional and tail (Märss et al. 2007).

Text figure 1.10 Reconstruction of a thelodont based on *Phlebolepis elegans* (Pander), not to scale (artwork by Dr Mark Witton).

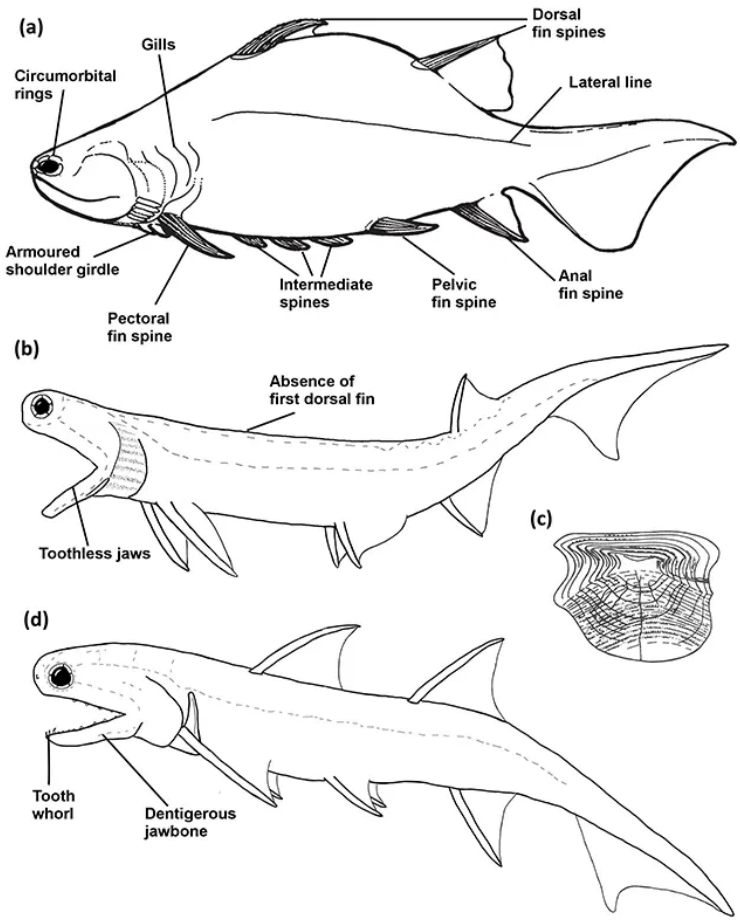
This range of scale morphologies helps researchers to determine whether the isolated denticles that they are describing are from a new taxon. The denticles themselves can be identified by looking at key features, such as the base, neck and crown morphology (Text-fig. 1.11). Both thelodonts from the DBB are scale taxa; this means that there is no known articulated material for *Paralogania ludlowiensis* or *Thelodus parvidens*.



Text Figure 1.11 Denticles of two thelodonts found in the DBB and their external morphology, not to scale (modified from Märss et al. 2007 fig. 17).

1.5.2 The Acanthodii

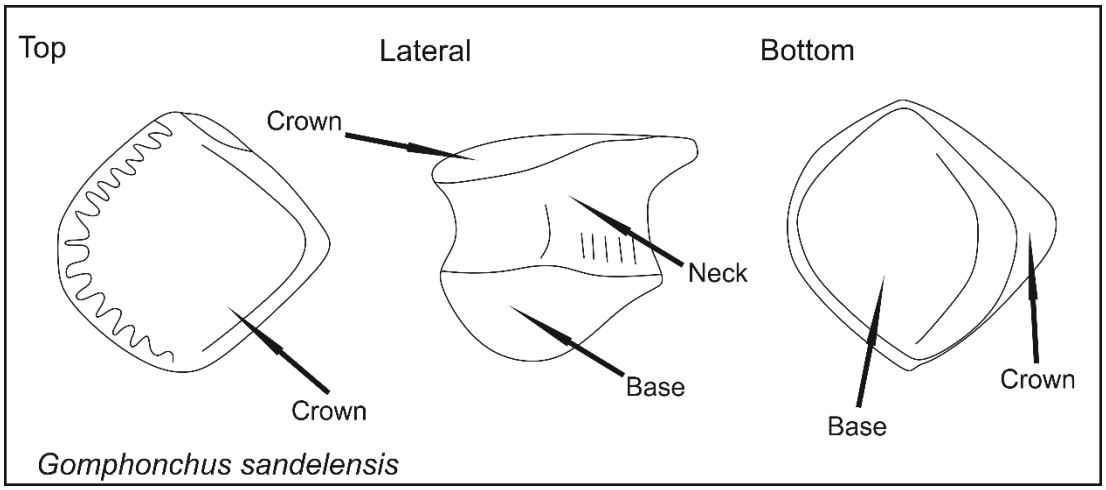
The gnathostomes (or jawed) vertebrates had appeared by the Silurian and were the first class to possess true gnathal (jaw) bones. The Acanthodii (Text-fig. 1.12) are known colloquially as “spiny sharks” because of their superficial similarities to sharks, with their sharp teeth and streamlined shape. Acanthodii is a paraphyletic group sharing characters of both bony and cartilaginous fish (Denison 1979; Zhu et al. 2013); they appeared in the Silurian Period and became extinct in the Permian (Denison 1979) having reached their zenith in the Devonian with a global distribution. Unlike the thelodonts, acanthodians had more ossified parts to their bodies most notably the fin spines and shoulder girdles.



Text figure 1.12 Reconstructions of three different acanthodians, showing generalised anatomy (a) *Ptomacanthus*, a climatiiform from the Devonian of the United Kingdom from Brazeau (2012); (b) *Howittacanthus*, an acanthodiform from the Devonian of Australia from Long (1986); (c) the scale of the acanthodiform *Acanthodes bronni*, showing acanthodian histology from Denison (1979); and (d) *Ischnacanthus*, an ischnacanthiform from the Devonian of the United Kingdom from Long (1986) (taken from Dearden 2015 Figure 1). Not to scale.

Like the thelodonts, the Acanthodii had a squamation, but this is a micrometric covering (tiny denticles). Acanthodii denticles have some key features that make them identifiable (Text-fig. 1.13). One is that the base of the denticle is often very rounded, which differs from the flat base of thelodont denticles. In the DBB Acanthodii denticles are also more ornamented on the crown than is seen in the thelodont taxa. Other differences are found between the two orders of Acanthodii.

The Ischnacanthiformes have ankylosed teeth within the jaw, while some of the Acanthodiformes seems to be unusual as, despite developing the first jaws, this order, lost its teeth and used its jaw to help filter feed. A previously recognised third order the Climatiiformes, had armoured shoulder girdles; however, this last order is no longer considered a cladistically valid group (Burrow pers. comm. 2017).



Text figure 1.13 External morphology of Acanthodii denticles (modified from Denison 1979, fig. 28), not to scale.

During the late Silurian acanthodians seem to have inhabited marine and freshwater habitats as well as marginal environments like deltas, tidal flats and lagoons (Denison 1979). The diet of acanthodians was more varied than that of the agnathan fish with which they shared the seas.

1.6 Contribution of research

During this study, a novel integrated technique for the processing of well indurated, low carbonate bone beds was developed and implemented to process the DBB (Hauser 2016). The study was a part of the larger IGCP 591 study on the 'early to middle Paleozoic revolution'. This project examined the gap between the Great Ordovician Biodiversification Event (G.O.B.E.) and the Devonian terrestrial revolution. Therefore, this study's contribution to the broader scientific community is of value as it fills a gap between the two other U.K. Silurian bone beds (the well documented Ludlow and less well documented Temeside bone beds). It is providing insights into how this environment in the late Silurian evolved and how it affected the fauna and flora at this crucial time in the history of life on Earth.

2. Methods

In this chapter the methods used in this project are described and discussed, including the paraffin expansion method (Hauser 2016; see Appendix A) and the first use of Milliput® for making peels of ostracods.

2.1 Field collection

The section at Weir Quarry was cleared using spades and shovels. Once this was carried out, chisels were used with hammers and pry bars to break the bed into manageable blocks for recovery, then, using wedges and crowbars, the blocks were levered out. Their way up was recorded and marked on the specimens and specimen numbers were added, then all were wrapped in paper and placed in boxes for transport. During this study samples were collected approximately every 24 cm along the exposure for a lateral extent of c. 8 m. At each point, the bed thickness was recorded, and at the beginning, middle and end of the exposure studied the dip and strike were taken.

To organise the samples collected from the DBB, a curation system was devised. The specimens have been given the code DBB. The samples that were used for lithological descriptions retained this code (e.g. DBB 7). The numerical value refers to the point within the quarry where the sample was taken (Text-fig. 2.1). If used for an ichnological study, they received an 'I' in the code (e.g. DBBI 2). For SEM micrographs, the code included also what size fraction it belongs to (e.g. DBB 7 500 for a sample from collection point 7 which came from the 500 µm size fraction). Macrofossil specimens were given the code (e.g. DBBM 2) with the "M" standing for macro and the numerical value being used if there were multiple specimens, as the sample location was recorded on the specimen itself. The prefix WQ is from early samples before a formal curation system was developed. The "S" prefix denotes a sample that was recovered from the Selfrag test residues.

Text figure 2.1 Exposure at Weir Quarry, showing sample collection points.

2.2 Sample preparation

2.2.1 Sedimentology

To study the sedimentology, standard c. 30 µm thick thin sections were produced by senior specialist technician Mr Geoff Long. A simplified method is as follows. The samples were impregnated (where necessary) with Buehler's EpoThin 2 two-part epoxy resin system utilising a vacuum chamber to draw the resin into the sample. The impregnated samples were bonded to glass using the same resin, then re-sectioned and ground to a thickness of 30 µm using a Buehler PetroThin machine. This method also, on occasion, presented an opportunity for the histology of some bioclast inclusions (denticles and spines) to be studied. Early in the project, attempts

were made to make simple histological slides. However, the department lacked the skills and facilities to make these thin sections, and the project lacked the funding to pay for samples to be made externally so this was abandoned, in favour of using the examples seen in the sedimentology thin sections.

The hand specimens were cleaned, using a cap full of Decon-90 detergent and a toothbrush, which lifted the soil, rootlets and fungal hyphae from the specimens. They were then washed off and left to dry. There were then handed to Mr Richard Hing if cut sections were needed.

2.2.2 Imaging

As this is primarily a micropalaeontology project, the imaging of the fossils was undertaken at the University of Portsmouth on scanning electron microscopes. A Jeol JSM-6100, Phillips XL 30 and a Zeiss EVO series MA10 SEM(s) were used with a working distance of 10 mm for the 212 µm material while the 500 µm samples had a working distance of 15 mm. The KV (kilovolts) setup varied depending on the fossil type that was being imaged and ranged from 10 to 20 KV, these ranges were used as it was the standard set up on the SEMs at the UoP and was a KV the author was familiar with having used the same setting during my undergraduate dissertation study on the Rhaetian Bone Bed. The higher KV values were used for close up work that required a better resolution and particularly small specimens. All samples that were placed in the SEM had been gold-palladium splutter coated.

While in the field images were taken on a Nikon D50 digital SLR and a Nikon Coolpix P50. For macro specimens such as the bivalves, gastropods and the sedimentology hand specimens, images were taken on a Nikon Coolpix P50 digital compact camera, with desk lamps used as a directed light source. The thin section images used in the study of the sedimentology, palaeontology and ichnology were captured using a Leica EZ4 W light microscope with a digital camera attachment. To produce maps for the thesis and to help with preparation for field work, Digimap was used. To produce many of the diagrams and plates within this thesis, Corel was used, in particular CorelDraw and Corel Photo-Paint.

2.3 Processing the Downton Bone Bed

2.3.1 Vertebrate palaeontology

Standard methods of processing bone beds, such as the use of 7-10 % acetic acid, were tried. However, because of the lack of any calcareous cement, this method was unsuccessful. This inability to break the host rock down presented a significant problem for the project. Experiments were carried out with other techniques such as freeze-thaw and Selfrag. Freeze-thaw was not used for the processing of the DBB, because the process is prolonged, and the author wanted to find a quicker method for extraction. Despite this, the method was used in the processing of the Ludlow Bone Bed (LBB). After the LBB sample had been placed in acetic acid and all of the carbonate had been dissolved, the remaining material was soaked in water for 24 hours then placed inside plastic containers, within a freezer. After a further 24 hours in the freezer, the samples were placed into a bowl, and boiling water was poured on top. They were then left to soak for an hour and then placed back into the plastic container and returned to the freezer. The material that had been released through this process was then poured into another bowl before sieving.

Selfrag was a novel technique that before this study, as far as the author is aware, had not been used to extract vertebrate microfossils. The method involved a kilogram of DBB being placed inside the Selfrag instrument with several sieves placed under the sample. Once the desired size fraction had been determined then the device was turned on, two electrodes pulsed the rock multiple times a second (this can be varied depending upon what you are trying to extract) with very high voltage $\leq$ 50,000 V. Once the processing had finished the door was opened and the sieves removed with each size fraction ready for picking or separation. A test sample of 1 kg was sent to Selfrag in Kerzers, Switzerland (where the company is based) and returned to the author to pick. The results were mixed. Although it had completely broken down the sample and the quality of fossils in the residue was suitable for further study, the cost of processing made it unsuitable. As a result, a method that would be as rapid as Selfrag but a fraction of the cost and could be done at the UoP was needed. As a consequence, an integrated method for breaking down well-indurated bone beds was developed the paraffin expansion method (Hauser 2016; see Appendix A).

The amount of DBB from Weir Quarry processed for vertebrate material was determined by assessing which pieces were likely to yield the most material. As mentioned previously, the DBB, like most bone beds, is laterally variable. Even within the c. 8 m studied there were some points along its lateral extent where no bone bed horizon was present and therefore this would not be efficient to process. Some samples, although good candidates for processing, were more valuable left whole as they contained macrofossils that needed to be studied. Overall, 16 kg of DBB were processed from 8 points of lateral exposure, which were 4, 5, 6, 7, 14, 18, 19, and 20 (Text-fig. 2.1). Once processed, the residues were passed through six sieves of varying mesh sizes: 2.36 mm, 1.70 mm, 500 µm, 212 µm, 106 µm and 76 µm. These were chosen as they would offer a broad range of sample sizes as well as enabling all but the smallest fossils to be collected. Once the residues were cleaned, they were placed in evaporating ceramic bowls and left to dry in a low-temperature oven.

To recover the phosphatic material from the rest of the residue, including the vertebrate remains, the use of heavy liquid separation was investigated. Often used in palynology and conodont study, sodium polytungstate (SPT) or lithium polytungstate (LPT), which are "heavy" liquids, are used. When the powdered SPT or LPT is mixed with distilled water, the amount of distilled water can be adjusted to vary the specific gravity (SG). Different minerals have different SG's. For separating vertebrate material, the SPT solution needs to have an SG of 2.8. In trying to use this method, several issues arose, one of which was that the right specific gravity could be challenging to maintain. This required the SPT to be warmed to allow the water to evaporate off; however, if too much water was released through evaporation, the process had to be repeated from the start by adding more distilled water. It also took up a lot of space, and with the high cost of the raw powder, as much as possible had to be reclaimed by filtering which took a great deal of time. Often, while waiting for the days that it could take to filter the 'dirty' SPT, the water content, and thus the SG would change, resulting in having to add more powder or more water to reach the desired SG. The other major issue with this method is that, unlike when using SPT to separate palynomorphs, the fossils all sink to the bottom of the tube leaving in most cases a sediment plug at the top making the pouring off process very difficult. This issue arose because many parts of the author's method were adapted from

palynology SPT methods as at the start of the PhD, there was no expertise within UoP SEES in micro-vertebrate processing. The bulk samples were picked using a small paintbrush dipped in water or propanol, to allow the denticles and spines to adhere to the brush; the concentrate was then picked for the best specimens and these placed onto SEM. stubs before imaging. The best material came from two size fractions: 212 µm and 500 µm. Either side of these fractions the material was either scarce or too severely damaged to be used for identification.

2.3.2 Taphonomic grade

As thelodonts are the most common and numerous fossil group in the DBB, they can be used as an indicator of certain aspects of the environment such as whether they have been transported far on the seabed for any length of time. By far the most common fossils are trunk scales of the thelodont *Paralogania ludlowiensis,* so this taxon has been used for establishing taphonomic grades (Text-fig 2.2; Table 2.1). A similar taphonomic grading system had been employed in the study of the Cliff End Bone Bed and the Keymer tile works in Lower Cretaceous Wealden of Hasting (Cook 1995). By grading the denticles 1-5, it should be possible to detect the overall quality of the denticles, and then how much energy and/or time they were exposed to

Usually, the entire range of taphonomic grades is used for specimens from the deposit in question, i.e. all fossils used are from the DBB at Weir Quarry. However, due to the state of preservation of the denticles in the DBB, there is not a near-perfect specimen to use as the highest grade (i.e. best preserved). Therefore, a denticle recovered from Linley Brook by Miller and Märss (1999, pl. 2, fig. 18), was used as an example of a very well preserved *Paralogania ludlowiensis*. All of the other figured specimens are from SEM imaging of the DBB.

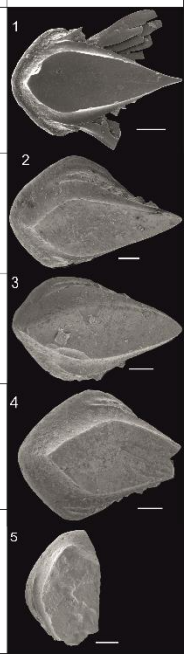
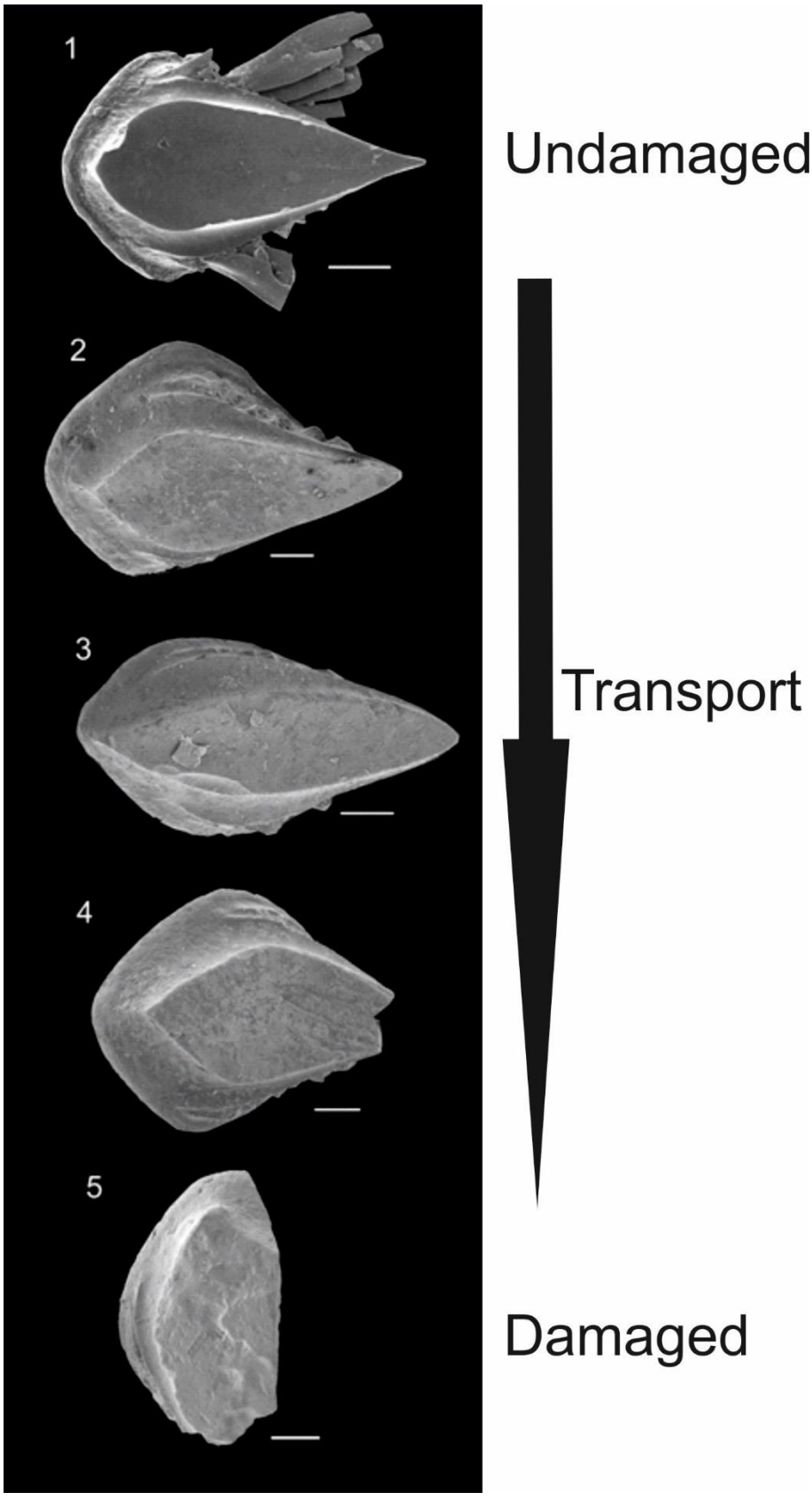
Grade		Image
1	Complete base, neck and crown with most spines and processes present, no abrasion on surfaces. N.B. image from Miller and Märss (1999)	
2	Complete base, neck and crown but no spines and processes present, no abrasion on surfaces.	
3	Near complete base, neck and crown but no spines and processes present, with a small amount abrasion on the surface.	
4	≥ 50% base, neck and crown with no spines and processes present, with a moderate amount of abrasion on the surface.	
5	≤ 50% base, neck and crown with no spines and processes present, with a moderate amount of abrasion on the surface. Positive identification may not be possible to genus level.	

Table 2.1 Taphonomic grades of *Paralogania ludlowiensis* denticles.



Text figure 2.2 Examples of taphonomic grade seen in Table 2.1, represents 100 µm.

2.3.3 Invertebrate palaeontology

The macroinvertebrates in the DBB comprise mostly gastropods and bivalves. These are poorly preserved in the DBB at Weir Quarry, and very little information could be gained apart from recording their size using digital callipers. To try to extract as much useful information as possible from the specimens, mechanical preparation techniques were used. A pneumatic air pen was used to remove matrix from around the fossils. A *Leperditia* (bivalved arthropod) was prepared using a needle as so not to damage the fossil when removing matrix. The micro invertebrates (brachiopods and ostracods) were mostly prepared by using the paraffin expansion method (Hauser 2016) as a by-product of processing for vertebrates. The micro invertebrates were then mounted and imaged on the SEM. The eurypterid and other macro specimens (gastropods and bivalves) were imaged using the macro settings on the Nikon Coolpix P50 digital compact camera. To reveal detail, directional light sources were used.

To study the ostracods it is common practice to produce silicone peels of the bedding planes which then capture the detail of the ostracod valves (Siveter 1982). The method involves creating a clay dam around the edge of the fossil to prevent any of the silicone leaking out. The silicone used in the method is Silcoset 105; it is a liquid silicone and requires a curing agent. Once mixed, the silicone is poured slowly and evenly into the mould preventing air bubbles from forming and is left to cure. Once set the clay dam is removed, the peel can be taken, then coated and placed on an SEM for study. This method, although standard, was not used in this study because the cost of Silcoset 105 is in excess of £100.

A new method was established. The first method tried was using liquid latex. Latex is commonly used to take peels of fossils (e.g. Waters 1983; Racheboeuf et al. 2008). The method follows the same steps as Siveter (1982) in that a clay dam is made around the edge of the bedding plane, to prevent latex from leaking away. The latex is then poured into the mould. The first to be poured is a thin latex; this records all the detail present in the fossils. The peel specimen is then gently tapped on a hard surface to remove air bubbles. Once it has nearly cured, a second thick latex is then poured on top, to strengthen the peel. The peel specimen is then tapped again to remove further air bubbles and left to set. The duration of this curing process is variable depending on various factors such as temperature and humidity. In the

sample used in this study, it took approximately 48 hours to cure. The dam is then detached, and the peel gently removed. The surface was checked for casts and impressions of ostracods using a hand lens.
Once specimens were found, the peel was cut to size so that it would fit on a 25.5 mm diameter SEM stub. It was then gold-palladium coated with 20 nm coating before being imaged on a SEM.
The second method tried was using Milliput®, which is usually used as a sculpting medium to repair fossils or to glue specimens back together. (Buttler and Stooshnov 2002; Andrews 2009; Beiner and Rabinovich 2013). What follows appears to be the first time that Milliput® has been recorded as a method to produce peels. Milliput® is an epoxy resin that is in a putty form; it is in two parts and must be mixed for it to cure. When it cures, it becomes hard, allowing it to record surface details such as the moulds of ostracod valves.

The two parts of Milliput® are cut in equal amounts and then mixed. Two types of Milliput® were used in this study: Milliput® standard and Milliput® superfine. The latter is designed to repair porcelain and was considered for use as its finer grain might allow for more detail of the valves to be recorded. In Milliput® standard, the two parts of the epoxy are different colours, and the instructions that come with the product indicate that the two parts should be mixed until they become one colour as a guide that the resin is well mixed. However, with Milliput® superfine, both parts are white, and the guidelines suggest that they should be kneaded for 5 minutes to ensure that a good mix has taken place. It is recommended that the user should wear gloves when mixing the Milliput®. The first attempts with this method were using Milliput® standard, and after they had been mixed, the Milliput® was placed directly on to the area where a peel was required. It was then left for approximately 4-5 hours before being removed from the specimen. The surface was checked for casts and impressions of ostracods using a hand lens. Once ostracods were found the peel was attached to a 25.5 mm diameter SEM stub. It was then gold coated with 20 nm coating before being imaged on a SEM. One issue that did arise from this was that because the Milliput® sets incredibly hard, it makes the peel challenging to remove without risking damage to either the fossil or the peel, with further development, perhaps a release agent could be used to aid in extracting the Milliput®.

The Milliput® superfine had to be mixed for longer, and the warmth generated from mixing the resin meant that it became friable. If placed on the site of interest and removed while still malleable (in an attempt to solve the issue of leaving the resin on until it set as mentioned above) it had a tendency either to record little detail or in some cases leave epoxy resin on the fossils and damaging the bedding surface. The solution was first to mix the Milliput® for 5 minutes; however, after that, the Milliput® was placed on a clean surface and left to cure partially. This had two effects: 1) to cool the Milliput® down, making it firmer; and 2) to allow the Milliput® to cure partially once again to firm up the Milliput®. The result of this was a medium that allowed for detail to be recorded, and it could also be removed from the specimen without causing any damage. The Milliput® was left for 1 hour and 10 minutes after kneading to get it to the right consistency, then it was pressed into the area of interest, and after a few seconds, it was then peeled off, carefully left on a sheet of flexible plastic, and left to cure fully. The flexible plastic was used as it allowed the peel to be removed quickly once cured. The surface was checked for casts and impressions of ostracods using a hand lens. Once the casts were found the peel was attached to a 25.5 mm diameter SEM stub. It was then gold-palladium coated before being imaged on a SEM.

The third medium used to produce peels was an A-silicone product developed for dentistry called PRESIDENT regular body, although similar products have been used in palaeontology before (Rose 1983; Galbany et al. 2006). As a silicone-based product, it requires a curing agent that is supplied with the product. Both the A-silicone and the curing agent are kept in separate tubes. The product comes in its applicator, which had a plastic nib, with a screw inside. Once loaded into the applicator and the trigger squeezed the two separates are mixed. It is then applied to the area of interest and left to cure. This is a swift process and took as little as ten minutes. It can then be removed; this causes no damage to the specimens. Unlike the latex or the Milliput®, being A-silicone, it will not adhere to an SEM stub using the usual carbon sticky disc. Instead, super glue was used to bond the peel to the 25.5 mm SEM stub. Before this was done, however, the surface was checked for casts and impressions of ostracods using a hand lens. It was then gold coated before being imaged on a SEM.

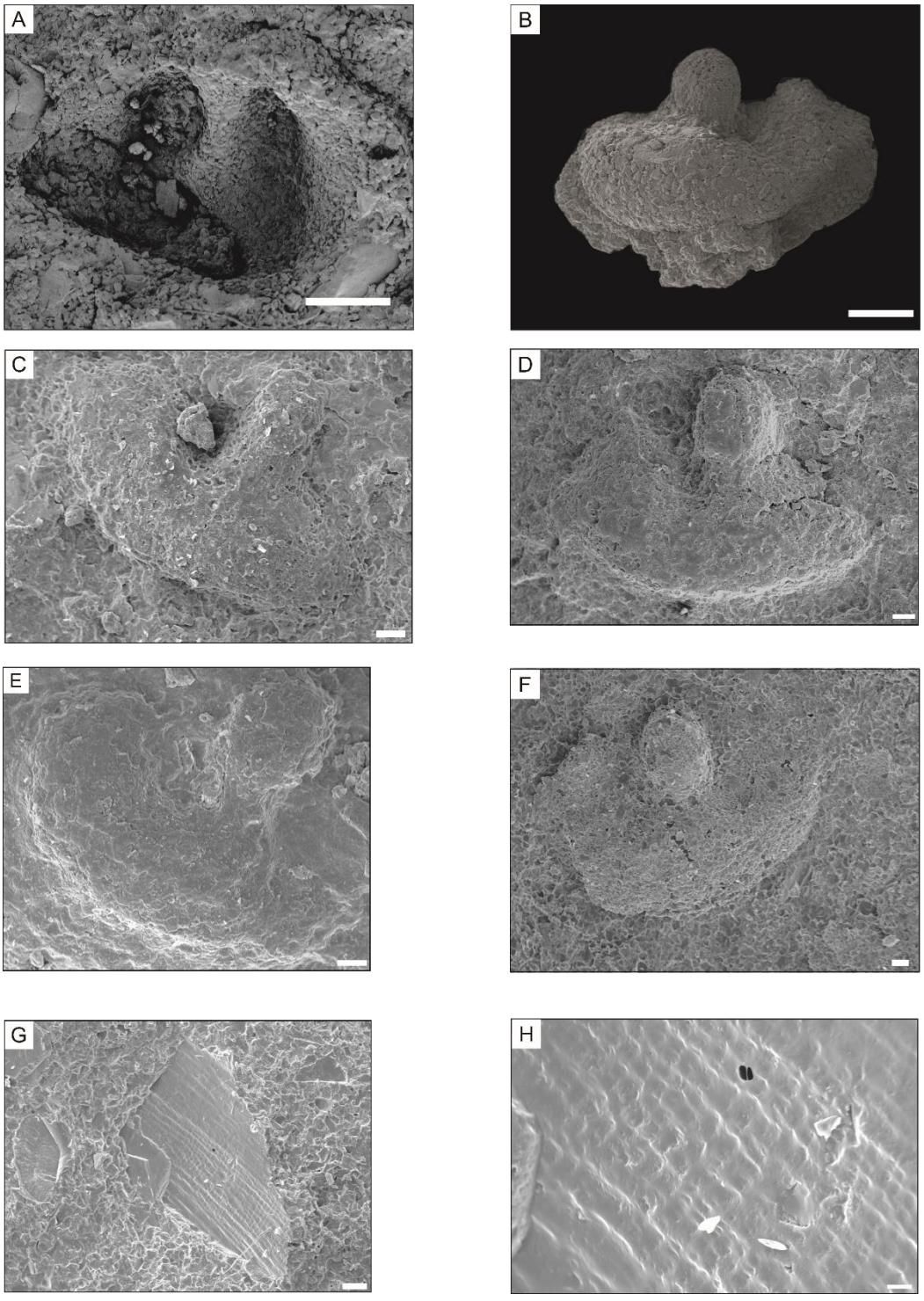
All of these alternative methods have pros and cons. The PRESIDENT regular body A-silicone method, although the quickest and easiest was also the most expensive. Each set of PRESIDENT regular body A-silicone costs around £50, which is still only half the cost of Silcoset 105. Latex, which is used for teaching by the UoP SEES was accessible and required no additional cost for this project. Although there is an outlay for the Milliput®, it is only around £5 which is a far more reasonable cost as multiple applications are possible from one box.

The most important aspect of this experiment in alternative methods to get ostracod is the quality of the peel. Plate 2.1 shows the results of each method used. What is clear is that none of the methods records exceptional detail of the ostracod valves. This is most likely due to there being a lack of detail present in the first place. Each of the methods was carried out on the same hand specimen of DBB. However, although the ostracod shown in images A-H is the same taxon, *Londinia arisaigensis*, they are not all the same specimen. In A the mould can be seen to be formed from tightly packed sediment, which holds the form of the valve, which has dissolved away. Image B shows that the valves liberated from the DBB by the paraffin expansion method (Hauser 2016) record the form and gross morphology of the ostracod valve. This cast allows for identification of the ostracod to genus and possibly species level.

In some cases, maybe even the sex of the valve can be determined from this method of study and imaging. Images C-F all show the same relative quality of the cast; it is possible to determine the genus and species, *Londinia arisaigensis.* Although no fine details can be seen on the casts this appears to be due to the preservation of the fossil and that information not being present to begin with. Image G shows a fragment of a lingulid brachiopod on the bedding plane; unlike the calcitic carapaces of the ostracods, its valves are made from calcium phosphate and have therefore survived diagenesis. This shows that where there are body fossils present a smooth, clean cast can be made.

Furthermore, in H, a close up of G, it can be observed that fine detail such as the growth lines and ornamentation on the valve is recorded by the PRESIDENT regular body. If that detail was present in the moulds of the ostracods in the DBB, then it would have picked it up. Instead, the detail was missing to begin with; therefore either the paraffin expansion method or using the Milliput® standard/superfine method is sufficient to study the ostracods within the DBB at Weir Quarry.

Plate 2.1



Explanation of Plate 2.1

Examples of ostracod peel experiments on the DBB. A) mould of *Londinia arisaigensis* as is found on bedding plane of the DBB. B) *Londinia arisaigensis* heteromorph DBB18 500 3, extracted using paraffin expansion method. C) DBB1 cast used liquid latex. D) *Londinia arisaigensis* Millitest 1, cast using Milliput® standard. E) *Londinia arisaigensis* DBB1, cast using Milliput® superfine. F) *Londinia arisaigensis* DBB7, cast using PRESIDENT regular body A-silicone. G) Brachio1 fragment of lingulate brachiopod on the surface of the DBB, cast using PRESIDENT regular body A-silicone. H) Brachio1 close up of Brachio1 showing growth lines and ornamentation, cast using PRESIDENT regular body A-silicone. Scale equals 100 µm A-G, H equals 20 µm.

2.3.4. Palaeobotany and palynology

The extraction of organic-walled fossils was carried out by Dr A. Butcher due to health and safety restrictions, although initial training was given so that the method was understood clearly. The standard method for palynological processing was used as described by Sutherland (1994) with some modifications by Dr A. Butcher. A description of this method was described by Dr R. Llewellyn in her PhD thesis and is as follows; "The samples were processed using a technique based primarily on Sutherland (1994), with minor adaptations by Anthony Butcher (pers. comm. 2011) described herein. Samples were cleaned using organic decontaminant (DeCon90) followed by treatment in an ultrasonic bath for at least 5 minutes. Samples were dried at room temperature and broken into approximately 10 mm sized chips. Approximately 50 g or 100 g of each sample was weighed and transferred to a polypropylene container where the following stages took place in a fume cupboard. Sufficient water to cover the samples was added to the containers. Small amounts (ca. 20 ml) of 37 per cent hydrochloric acid (HCl) were added to the container until effervescence ceased, in order to remove carbonate material. Containers were then filled with water and left to settle overnight. Once settled, the water was slowly decanted off into a calcium hydroxide neutralising solution and refilled. This process was repeated four times in total. 50–70 ml of 58–62 per cent hydrofluoric acid (HF) were added to each sample to remove silicate material, and left for at least 48 hours to react. Samples containing HF were agitated gently several times a day (at least twice) to prevent a reaction 'crust' layer forming on top of the sample residue, which may have prevented reaction of the acid with the residue beneath. After the desired reaction time had passed, the sample containers were filled with water, left to settle, and decanted a total of four times as described above.

To ensure that no fluoride ions remained in solution, a small amount of HCl was subsequently added to each sample. Neutralisation was undertaken as for the previous stages, and the decanting and settling processes continued until the liquid in the samples container tested pH neutral with universal indicator solution. The addition of sodium carbonate was occasionally used to speed up neutralisation where samples were still acidic after several decants. Minor amounts of sodium carbonate were added to the containers to neutralise samples and ensure they did not become alkaline. Samples treated with sodium carbonate were not left to settle overnight and were immediately removed from the fume cupboard for the next stage of processing. This prevented sodium carbonate from inhibiting the settling out of finer material held in suspension.

After the samples and the container had both been neutralised, they were removed from the fume cupboard and sequentially sieved through a 53 μm and 10 μm nylon sieve mesh. The organic material from both fractions was separated using the heavy liquid sodium polytungstate, at a specific gravity of 2.0–2.1 with at least 3 separations carried out to ensure good recovery of specimens (Gelsthorpe 2002). Separations continued until specimens could not be viewed within the meniscus of the heavy liquid."

In total 900g (50g in each sample) was processed using the Sutherland/Butcher method. The processed residues were sieved by the author, Dr A. Butcher, Mr R. Hing and Mrs E. Dyer using palynology sieves with 500, 53 and 10 μm meshes. The organic residues were then picked onto stubs. Initially a standard SEM stub of 12.2 mm diameter was used; however, due to a large amount of material and the time constraints of the project, a larger 25.5 mm stub was used so that part of the sample could be "strewn" across a wider surface area. This had two benefits: 1) to allow more material to be looked at and 2) to allow the specimens more space so that when looking at them using the SEM, samples were not piled up on top of each other. Additional organic-walled fossils, especially plants, were extracted via the paraffin expansion method (Hauser 2016).

3. Sedimentology

3.1 Introduction

The sedimentology of the DBB at Weir Quarry indicates the depositional environment. The chapter also discusses fieldwork carried out to establish the current known extent of the DBB and the quality of the exposures in the Ludlow and Downton Gorge area, which were first recorded in relation to the DBB by Elles and Slater (1906).

3.1.1 Previous work

Very little work has been carried out on the sedimentology of the DBB; but, the Downton Castle Sandstone Formation (DCSF) that contains the bone bed has been intensively studied. The first investigation was by Murchison (1839), who used broad-brush terms such as "Downton-Castle Building-stone, greenish grey, slightly micaceous sandstone". However, he does go on to record the discovery of bone beds in the upper Ludlow deposits.

Elles and Slater (1906) were the first and only authors to provide an in-depth study of the rocks including the DBB. They stated that two feet above the level of the road (assumed here to be the Whitcliffe Road) the *Platyschisma*-bed (*Eb*) has a 'bony' appearance and passes laterally into the DBB. They also record the DBB cropping out westwards towards Downton Castle, and further to the southwest along the same track that the LBB can be seen.

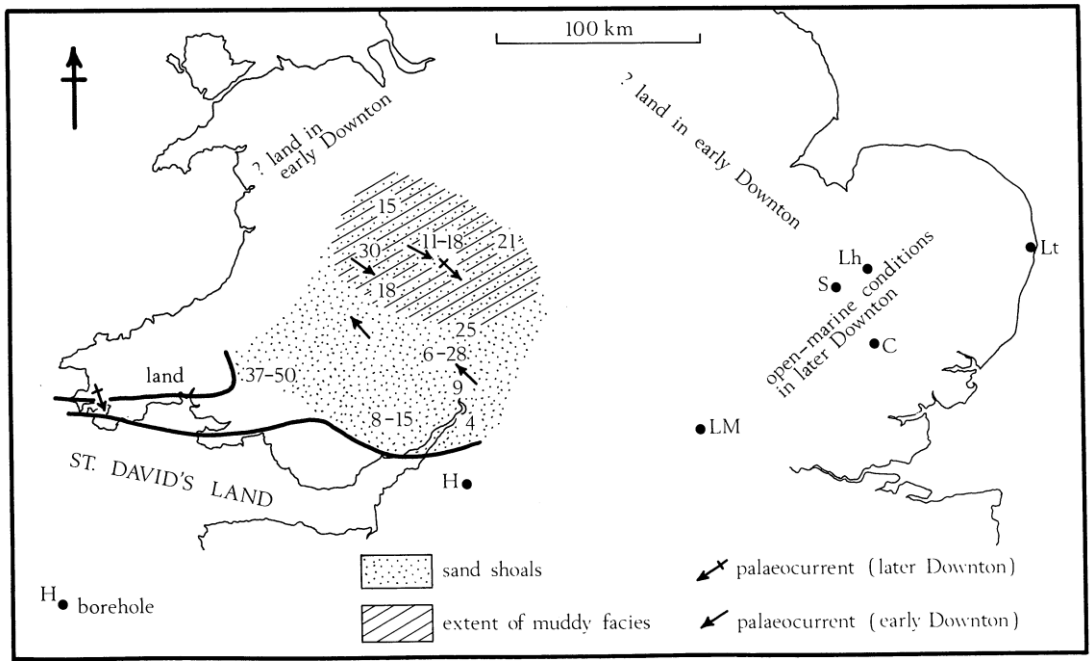
Stamp (1918) gave general summaries of the sedimentology, describing the Downton Castle Sandstone Series as "Grey shales with bands of sandstone and Platyschisma limestone (=Platyschisma shales)". He described the geology as looking unlike anywhere nearby. Of note is Stamp's reference to the DBB in which he states, "These silvery shales are succeeded by the *Platyschisma* Band which is here, in addition, a bone-bed (the Downton Bone-Bed).". Stamp (1923) commented "The sequence in the Linley Brook was described many years ago by Roberts & Randall. The bed they called the "Lower or Ludlow Bone-bed" is the Downton Bone Bed of Elles and Slater." Stamp (1923) noted that the true Ludlow Bone-bed occurs a few feet lower in the "hard calcareous shales with fish-remains".

Whitaker (1962) visited some of Elles and Slater's localities and collected samples, as well as mentioning the good exposure of the DBB at Weir Quarry (SO 4561 7524). He suggested, based on the fossil assemblage and work done by Denison (1956), that the fossils represent a nearshore fauna. Holland et al. (1963) listed three localities at which the DBB can be seen: their locality 57 (SO 4449 7427), initially described by Elles and Slater (1906); locality 136 (SO 4557 7403) and locality 137 (SO 4449 7427). Allen and Tarlo (1963) gave a facies interpretation of the Downton Castle Sandstone Group. They described a lithology that seems similar to the DBB as seen at Weir Quarry, "Yellow sandstones above: scour-and-fill, cross-bedding. Flat-bedding, current ripples. Bone beds: shells, phosphatic debris. Green siltstones below: current ripples, lamination. *Lingula* and abundant molluscs". They interpreted the environmental setting as "near-shore to beach: silts formed offshore within wave base overlain by transgressive sand shoals and beaches. Turbid often brackish water." They compared the succession of the Downton Castle Sandstone Group with modern deltas, e.g. the Mississippi, Rhone and Niger. Allen (1974) gives a detailed description of the Downton Castle Formation (hereafter to be referred to as DCSF as latter is synonymous with the Downton Castle Formation), later renamed Downton Castle Sandstone Formation (hereafter DCSF). He included detailed descriptions of the facies observed within the DCSF. He commented on the texture and composition of the mudstones and shales, within his Table 1 (p. 78) showing that the clay mineralogy of the DCSF contains illite, chlorite and occasional kaolinite. The DCSF comprises mostly green shales with secondary mudstones. He noted that they rarely contain more than 20 % of either clay or sand grade material; this is shown in his figure 2 (p. 79). Part of the paper details the sedimentary facies and environments of the DCSF. He discussed the climatic setting, suggesting a warm to hot climate with mean temperatures between 16° C and 20° C as well as seasonally distributed rainfall with mean annual rainfall estimated at 100-500 mm.

Antia (1980) continued this investigation into the sedimentology of the Ludlow section of the DCSF as well as the LBB across the Welsh Borderlands. He looked at the different facies present at the type section of the LBB at Ludford Lane. Strangely, he does not mention the DBB, although within his facies C description, he does mention several of the invertebrate and plant fossils that are associated with the DBB, but there is no reference to vertebrates. Bassett et al. (1982) reappraised the

geology of the Welsh Borders with the focus being on defining the Downton Series as the fourth series of the Silurian System. They provided brief sedimentological descriptions of the DCSF, describing the PSM as c. 2 m of olive mudstones and siltstones, with laminated bone sands. They do not refer to the DBB, but they list many of the fauna and flora found in the PSM. Allen and Richardson (1985) discussed the transition from marine to freshwater facies in the Anglo-Welsh basin, and produced a model of palaeocurrents during the Downton (late Ludlow-Přídolí) Series sedimentation in southern Britain. They suggest that the palaeocurrent would have flowed in a southeast direction with possible land in the northwest (Text-fig. 3.1).

The DBB at Linley Brook was studied by Bradfield and Tucker (1986) who proposed a new division of the DCSF: instead of the three previously recognised members, they divided the DCSF into the Ludlow Bone Bed Member, Siltstone Member, Downton Bone Bed Member and the Sandstone Member. They suggested that the DBB at Linley Brook is laterally equivalent to the DBB at Downton Castle.



Text figure 3.1 Palaeocurrent during the Downton (Přídolí), taken from Allen and Richardson (1985).

Smith & Ainsworths (1989) noted hummocky cross-stratification in the DCSF. Evidence that the beds were formed through storm activity on a shoreface as opposed to a tidal or tidal mud flat. They also point out that the lack of articulate brachiopods and the general lack of open marine fauna suggests that the Downton Group was laid

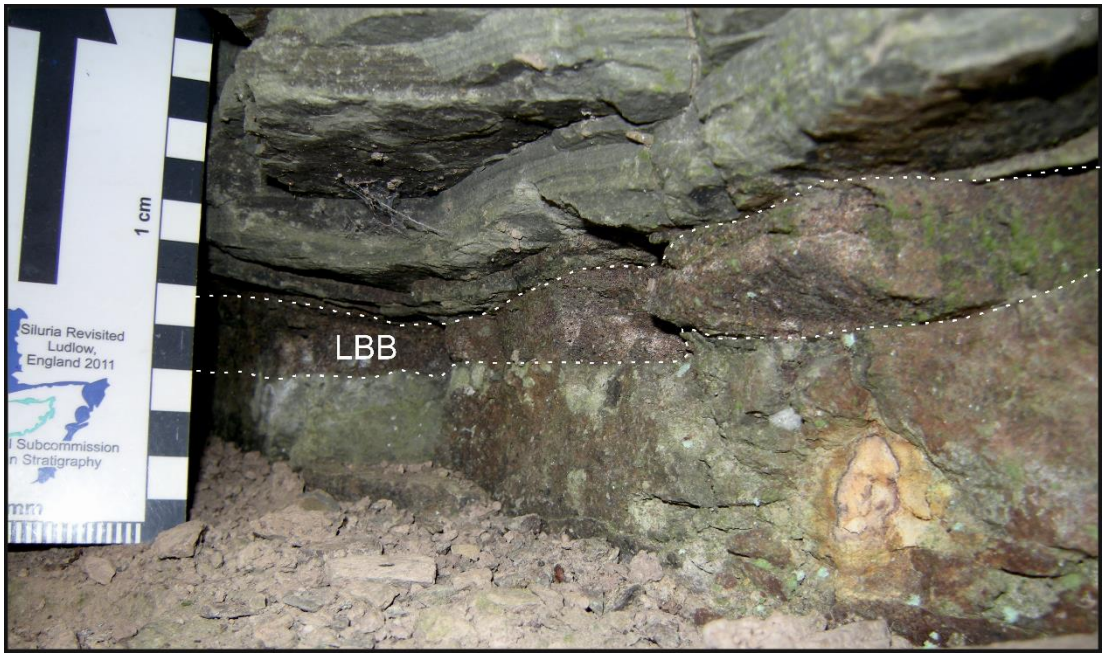
down in a restricted Downton Sea (the size of which they suggest may have been akin to the present Lake Huron; c. 60,000 sq. km) before the Acadian uplift eliminated the Downton Sea. It has also been suggested (Schmitz 1992) that the sediments of the DCSF and the Ludlow Bone Bed Member (LBBM) show evidence of an increase in iridium and that there are similarities between the hummocky cross-stratification of the Downton Group and the storm beds of the K-Pg boundary of Brazos River, Texas. The inference is that a bolide impact may have enriched the LBB in iridium.

Cherns et al. (2006) discussed many aspects of the lithostratigraphy, biostratigraphy and facies changes in the borderlands during the Silurian. Most other papers that describe the sedimentology of the DCSF or the PSM do so, for the most part, only within the geological setting sections of fossil flora or fauna papers, or in papers on other topics (i.e. Turner 1973; Dunlop 1996; Miller 1995a; Miller et al. 1997; Miller and Märss 1999; Glasspool et al. 2004; Märss and Miller 2004; Loydell and Frýda 2011).

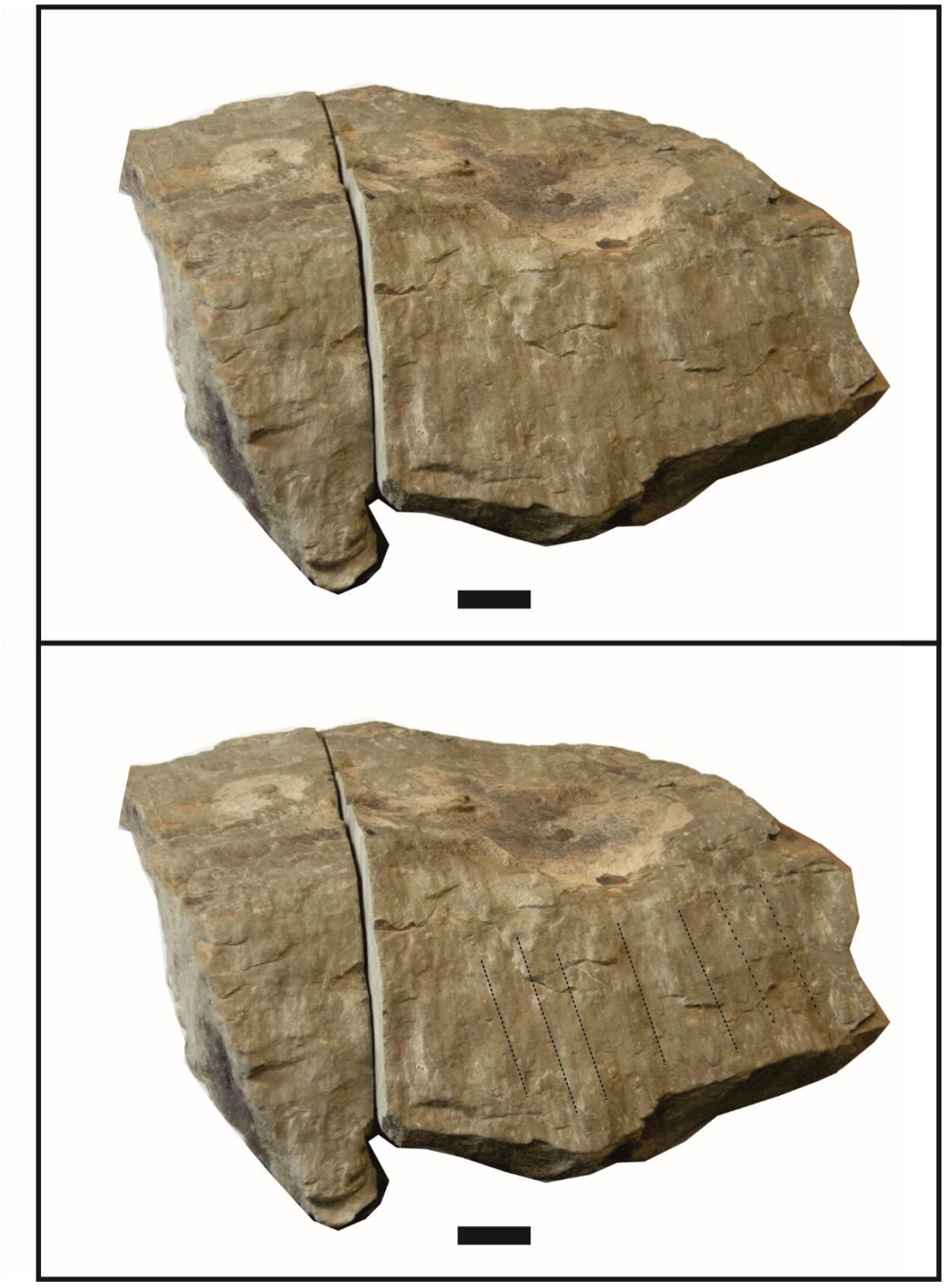
3.1.2 Outcrop description

The lateral extent of the outcrop examined at Weir Quarry is *c.* 8 m, while the vertical extent is *c.* 1.87 m (Text-fig. 3.2). On the north side of the path into Weir Quarry the upper part of the Upper Whitcliffe Formation (UWF) and overlying LBB can be seen (Text-fig. 3.3). To access the LBBM bed within the quarry, however, requires digging down to expose the beds. The discrepancy is explained by a sample of rock collected at the entrance of the quarry 105 cm above the base of the LBB (Text-fig 3.3). It is highly polished and has striations which are interpreted as slickensides (Text-fig. 3.4) providing evidence of faulting. The beds that would contain the LBB have been downthrown to the north. Allen (1974) recorded the presence of a fault in the area, related to the Church Stretton Fault complex; however, it is clear that there are also many minor faults. According to Elles and Slater (1906), the DBB is *c.*1 m above the LBB. The distance between the DBB and the base of the overlying Sandstone Member provides the most assistance in locating the DBB at Weir Quarry. The DBB is *c.* 54 cm (with some lateral variability) below the base of the Sandstone Member.

Text figure 3.2 Inside Weir Quarry showing the exposure of the DCSF, with its members indicated: Ludlow Bone Bed Member (LBBM), Platyschisma Shale Member (PSM) and the Sandstone Member (SM).



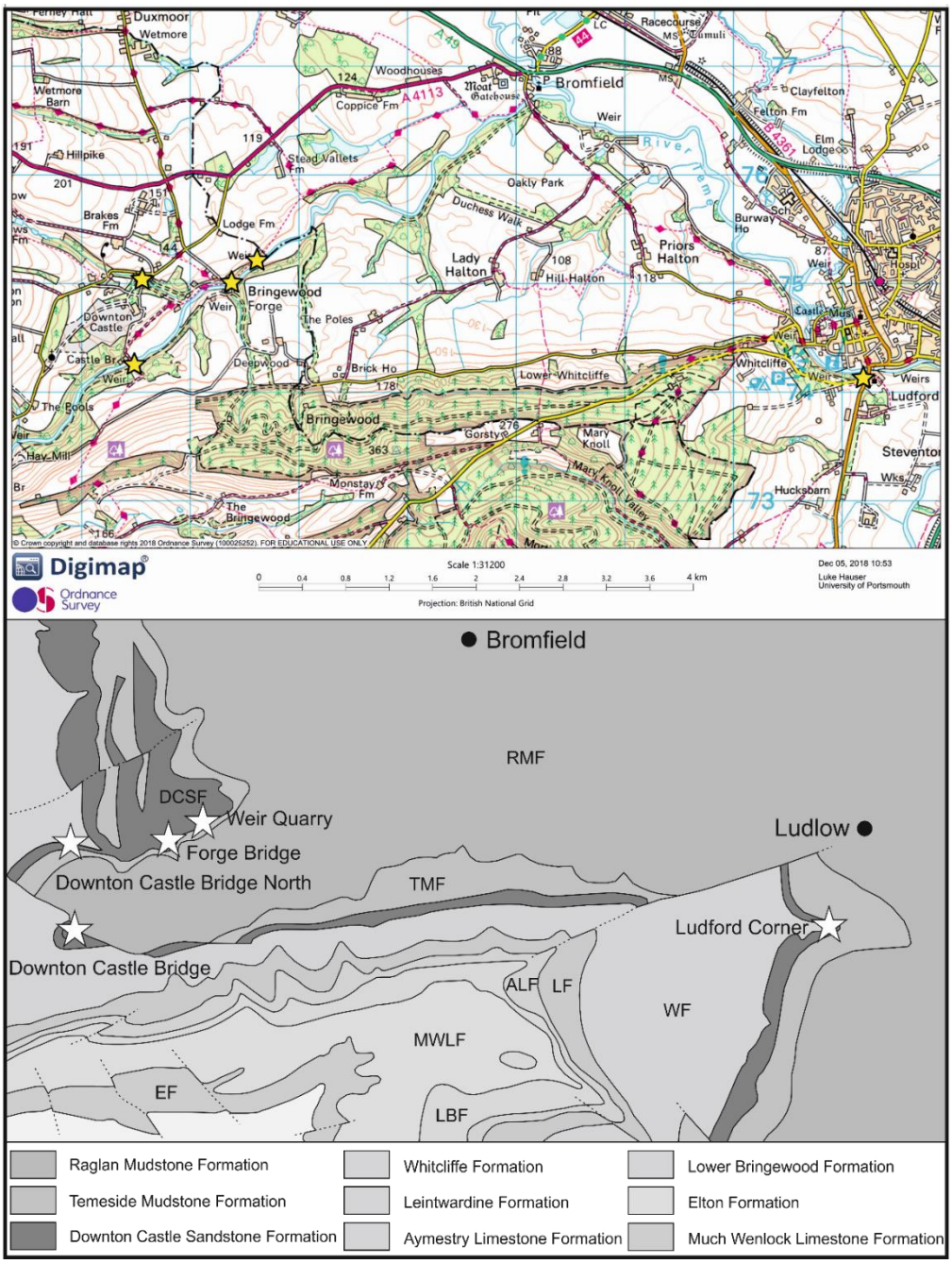
Text figure 3.3 The LBB at Weir Quarry adjacent to the path; dashed line represents lower and upper boundaries of the LBB, with UWF below and DCSF above.



Text figure 3.4 Sample from Weir Quarry with slickensides picked out (lower figure) collected from 1.05 m above the base of the LBB (SO 4563 7523). Scale bar represents 1 cm.

3.1.3 The local extent of the Downton Bone Bed

As discussed above, the bulk of research on the DBB prior to this study was carried out by Elles and Slater (1906). As part of their work, they traced beds across the Ludlow district. With reference to the DBB, they discussed three key localities: Ludford Lane, Forge Bridge and Downton Castle Bridge (Text-fig. 3.5). Having visited these localities, the current state of the outcrops used initially to describe the DBB is discussed below.



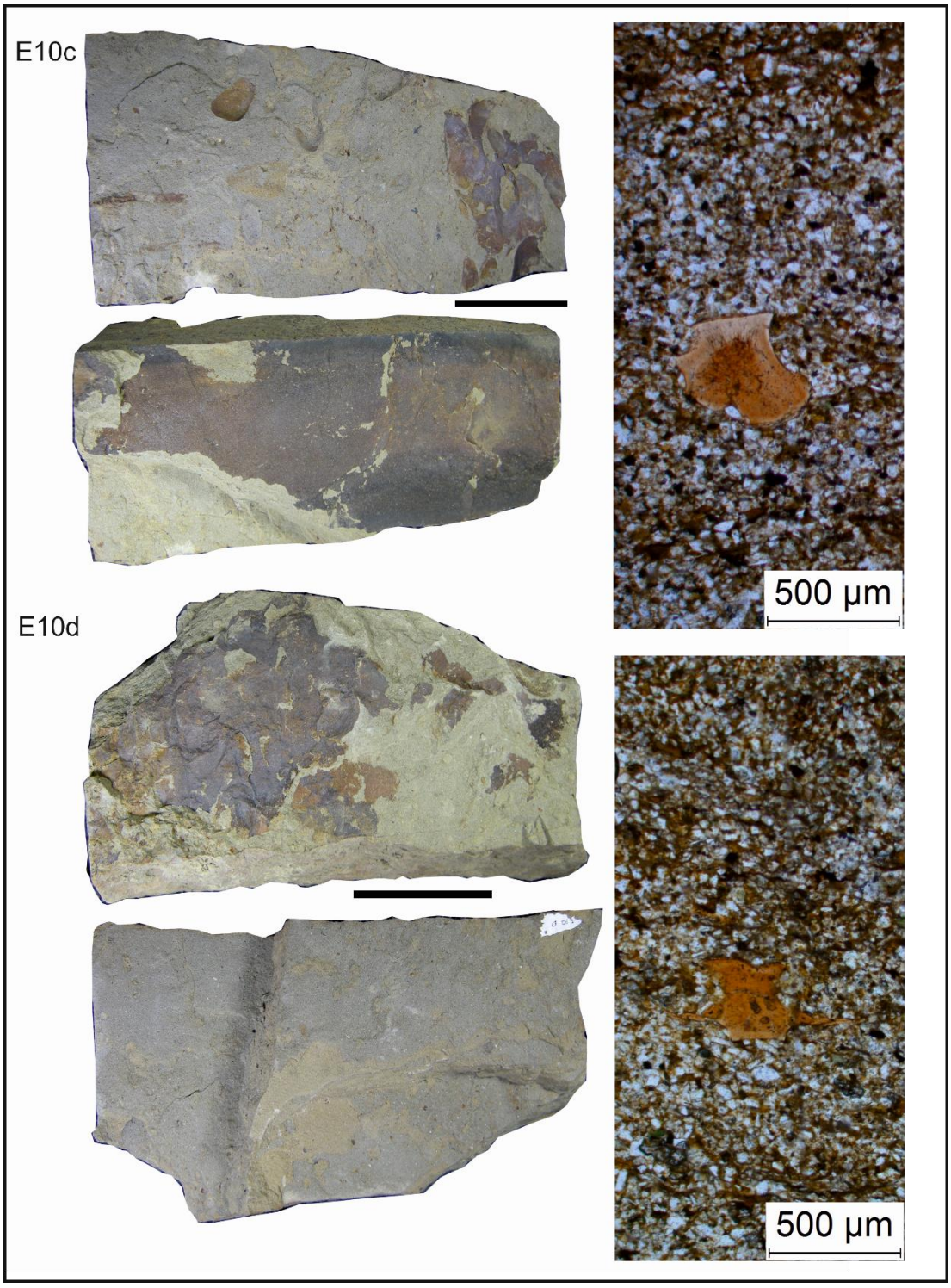
Text figure 3.5 Local area of DBB studied above with underlying geology below; stars indicate localities (Modified from Digimap 2018).

3.1.3.1 Ludford Lane

Ludford Lane is the natural starting point as this is where the bed (E*b*) hosting the DBB was first recognised, the Platyschisma Bed. Elles and Slater (1906) reported a "bony-tendency" within the bed (Text-fig. 3.6). The sample of E*b* (A378502) shown in Text-fig. 3.6 is very similar to the material from Weir Quarry. The sample appears to have been collected along Whitcliffe Road (Text-fig. 3.7). However, material collected during the late 1980s resulting from a road-widening scheme (housed in the Ludlow Museum Collections Resource Centre) is quite different. Samples E10c and E10d (Text-fig. 3.8) were reported to be collected from horizon (E*b*) of Elles and Slater's stratigraphic scheme, and although thelodont denticles are present in the upper and lower part of the samples, they are in low abundance and are not associated with the ostracod and brachiopod fauna seen in the original samples. This discrepancy could be accounted for either by the bed being laterally variable, or by subsequent collectors not sampling specifically Bed (E*b*) or at the same level within the bed. As collecting is prohibited and because the sample was not found *in situ*, identifying the true sampling point is unlikely be resolved.

Text figure 3.6 Upper left, sample A378502 from the Sedgwick Museum of Earth Sciences, Cambridge collected by Elles and Slater 1906; scale 5 cm below is close up of A378502, thin sections of A378502 revealing the "bony" tendency of Bed E*b*, Th= thelodont and Br= brachiopod.

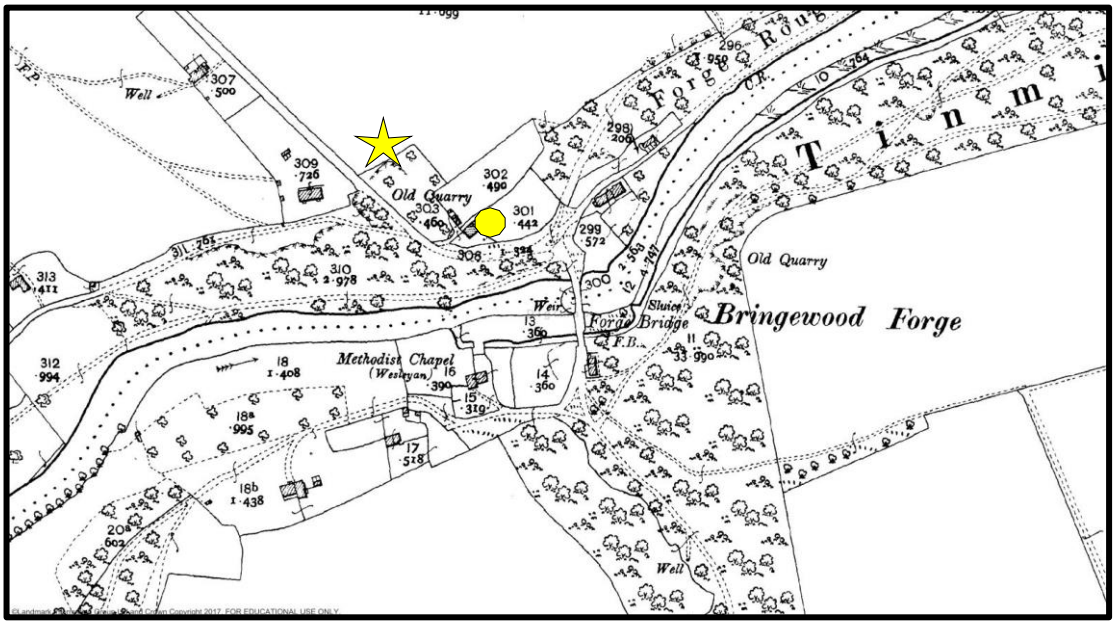
Text figure 3.7 Whitcliffe road (SO 51214 74143) where sample A378502 was collected; the area is now densely vegetated.



Text figure 3.8 Samples E10c (top) and E10d (bottom) collected during the Whitcliffe Road expansion during the 1980s, housed in the Ludlow Museum Collections Resource Centre. Unlabelled scale bars represent 5cm.

3.1.3.2 Forge Bridge

Forge Bridge is the most enigmatic of the three Elles and Slater localities. Despite the large amount of material held at the Sedgwick Museum of Earth Sciences, Cambridge (collected by Elles and Slater) there is none stated to be from Forge Bridge, even though Elles and Slater produced a stratigraphic cross section here (their fig. 5, p. 210; Text-fig. 1.6). They described a transition within the Platyschisma Bed, saying that it takes on the full "characteristics" of a bonebed. Unfortunately, they did not specify the locality of this critical transition; they described a "cottage" but no more specific information. On modern maps there is a building close to Forge Bridge, referred to as Forge Cottage, and it is the only cottage in the geographical range referred to by name suggesting that it is a local landmark. The 1900's map (County series 1:2500, 1st revision, Shropshire, 1903) shows (Text-fig. 3.9) an old quarry located just behind Forge Cottage, which is most likely the Forge Bridge locality.



Text figure 3.9 Map from the 1900s showing the old quarry (star) located just behind Forge Cottage (circle) (Modified from Digimap 2019).

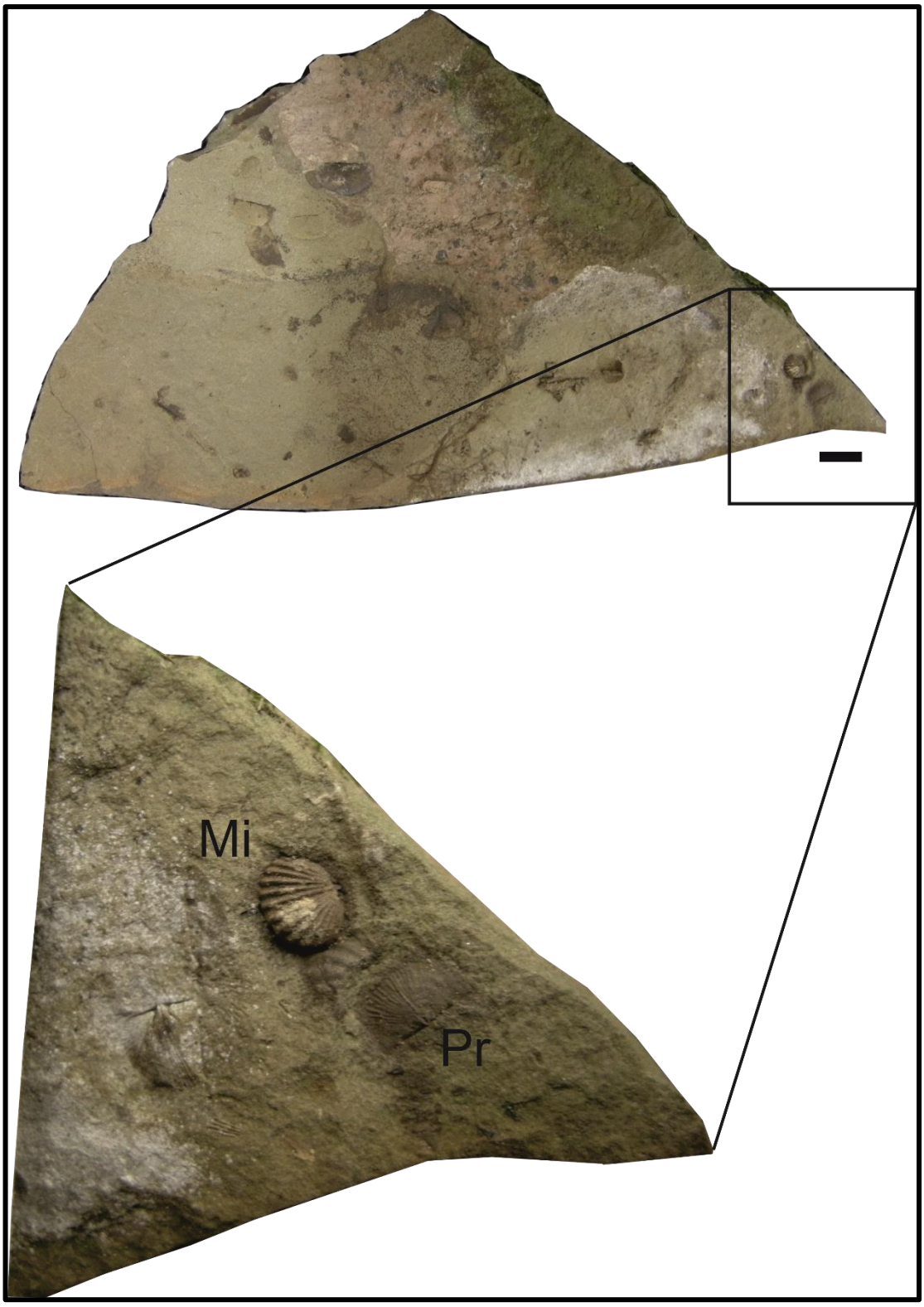
The SSSI protection of Downton Gorge does not apply to this site which is noticeable by its fill of domestic waste. Despite this, the locality shows an excellent outcrop of the Sandstone Member (Text-fig. 3.10).

Text figure 3.10 c. 5 m of outcrop of the Sandstone Member of the DCSF at “Forge Quarry” (SO 45287 75067).

However, the lower two members of the DCSF are now below the current floor of the quarry and to access these beds would require a JCB to dig down. It is easy to imagine that c.113 years ago when Elles and Slater were in the area they might have visited and seen the DBB.

Text figure 3.11 Road section at Forge Lane; scale 15 cm (SO 45367 75023).

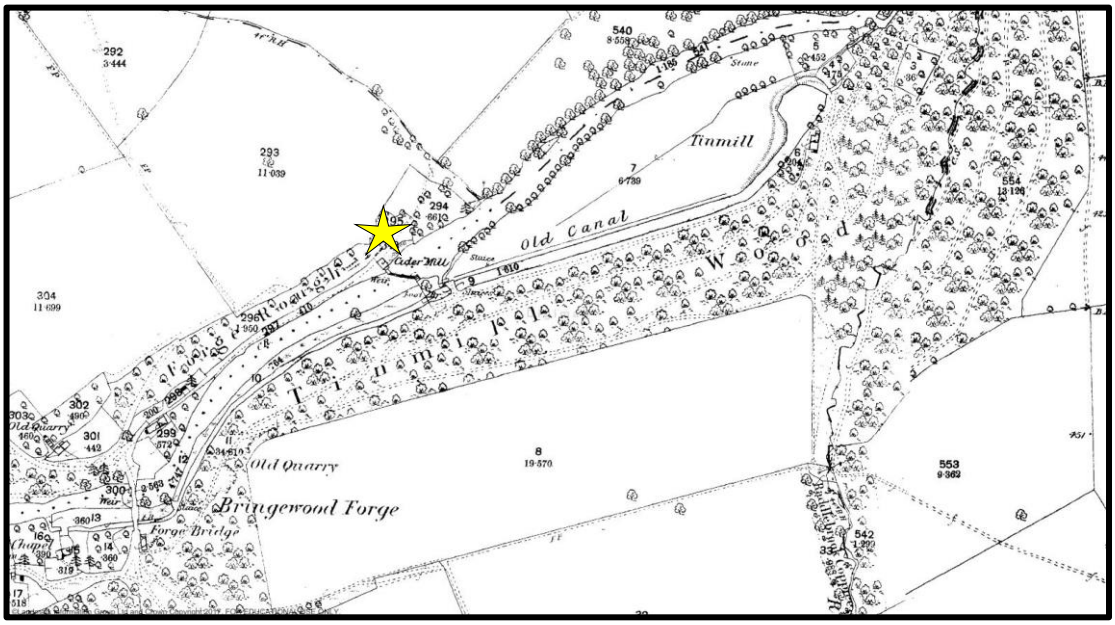
This inference is further supported by fossils found in the road section below Forge Cottage, at 21 cm and 30 cm above the visible section (Text-fig. 3.11): brachiopods, in particular, *Protochonetes* sp. and *Microsphaeridiorhynchus nucula* (Text-fig. 3.12). This shows that at this level the beds are part of Elles and Slater's D unit, the "Upper-Whitcliffe or *Chonetes*-Flags" bed (D*a*) (Text-fig. 1.7, p. 23) and that the Ludlow and Downton Bone Beds must be above this. These brachiopods are not recorded from the PSM, but do fit with fauna recorded by Elles and Slater for the *Chonetes*-Flags.



Text figure 3.12 Brachiopods: (Pr) *Protochonetes* sp.; (Mi) *Microsphaeridiorhynchus nucula*, collected from the road below Forge Cottage shown in Text-fig. 3.11; the scale bar represents 1 cm.

Within their Downton-Castle Inlier section, Elles and Slater (1906), discussed the Ludlow Bone Bed as "being seen in the road leading to the bridge [Forge Bridge] along a track leading to Forge Rough" (this is in the direction of Weir Quarry). They go on to say, "and again farther to the north-east, close to a cottage by the Old Millrace-weir". They then describe the Temeside Group and start by mentioning the Platyschisma-bed (E*b*), "at all these localities [it is unclear which localities they are referring to] the Platyschisma-bed (E*b*) is found in its usual position, with the intervening 3 feet [c. 1 m] of mottled sandstone between it and the Ludlow Bone-Bed". Adding that "in the road [again they do not state which road] section it is slightly 'bony' in character; but at the Cottage it has taken on all the characteristics of a bone-bed, and so closely resembles the Ludlow Bone-Bed that it can only be distinguished by the presence of *Platyschisma*, which still occurs abundantly and has never been found by us at the lower horizon".

The locality that Elles and Slater describe as the transition from the Platyschisma-bed (E*b*) to the DBB is by the cottage at Old Millrace-weir. Based on their description and maps from the 1900s (County series 1:2500, 1st revision, Shropshire, 1903) (Text-fig. 3.13) this would point to Weir Quarry as the possible site for this original description of a transition, as it's the only easily accessible site near to a weir, and the weir is the only one near Old Mill Race.



Text figure 3.13 Map from the 1900s showing the landscape when Elles and Slater carried out their fieldwork. The star locates Weir Quarry (Modified from Digimap 2019).

There is still some confusion however, as samples collected in this PhD project from the DBB at Weir Quarry are not as fossiliferous as one might expect based on Elles and Slater's description. The fact that no samples could be collected from Forge Bridge to determine the nature of the DBB at this point makes it difficult to assess whether Elles and Slater were referring to Weir Quarry as the site of the transition or if it could be seen at Forge Bridge. While it can be seen in the study that the material from Weir Quarry is more abundant than at Ludford Lane it could not be described as to "so closely resemble the Ludlow Bone-Bed that it can only be distinguished by the presence of *Platyschisma"* (Elles and Slater 1906, p.210).

3.1.3.3 Downton Castle Bridge

Downton Castle Bridge is another locality mentioned by Elles and Slater (1906). They stated "Two feet above road-level the *Platyschisma*-Bed (E*b*), which is here ' bony,' may be noted (= Downton Bone-Bed)". This bony appearance can be seen from their uncatalogued specimen (SM.X50294) (Text-fig. 3.14) in which the vertebrate material is extensive and shows a range of colours, including black which makes it stand out against the olive colour of the host rock. Today the exposure, like many of these historic and scientifically important sites in the Welsh Borderlands, is in a poor state. Trees grow out of the exposure (Text-fig 3.15), and a slope of overburden covers c. 4 m of what may initially have exposed the Sandstone Member.

Text figure 3.14 Sample X50294: rock sample (upper) and thin section (lower) from the Sedgwick Museum of Earth Sciences, collected at Downton Castle Bridge by Elles and Slater. The scale bar in the upper figure represents 5 cm.

Text figure 3.15 Section at Downton Castle Bridge (SO 44478 74268).

3.1.3.4 Miller's locality 14c

Above the bridge to the south along a track is another locality (SO 4442 7402). It was visited by Holland et al. (1963) who commented on the appearance of the DBB and samples were collected for processing by Jeppsson in 1968. However, Miller (1995b), who also visited the site (locality 14c), reported that the beds were no longer exposed as of December 1983 (Märss and Miller 2004; in which they refer to the site as locality 12). Having visited the locality, it is confirmed that the exposures are no longer present and now appear to have been cleared for agriculture. At the side of the tracks revealed by digging, there appears to be evidence of the underlying geology. Despite this, beds of significance appear to have been removed (Text-fig. 3.16).

Text figure 3.16 Locality 14c (SO 4442 7402) of Miller (1995a). The exposure that was present, as described by Miller (1995) has gone, with only the lower part of the section revealed by digging under the turf. Scale represents 15 cm.

3.1.3.5 North of Downton Castle Bridge.

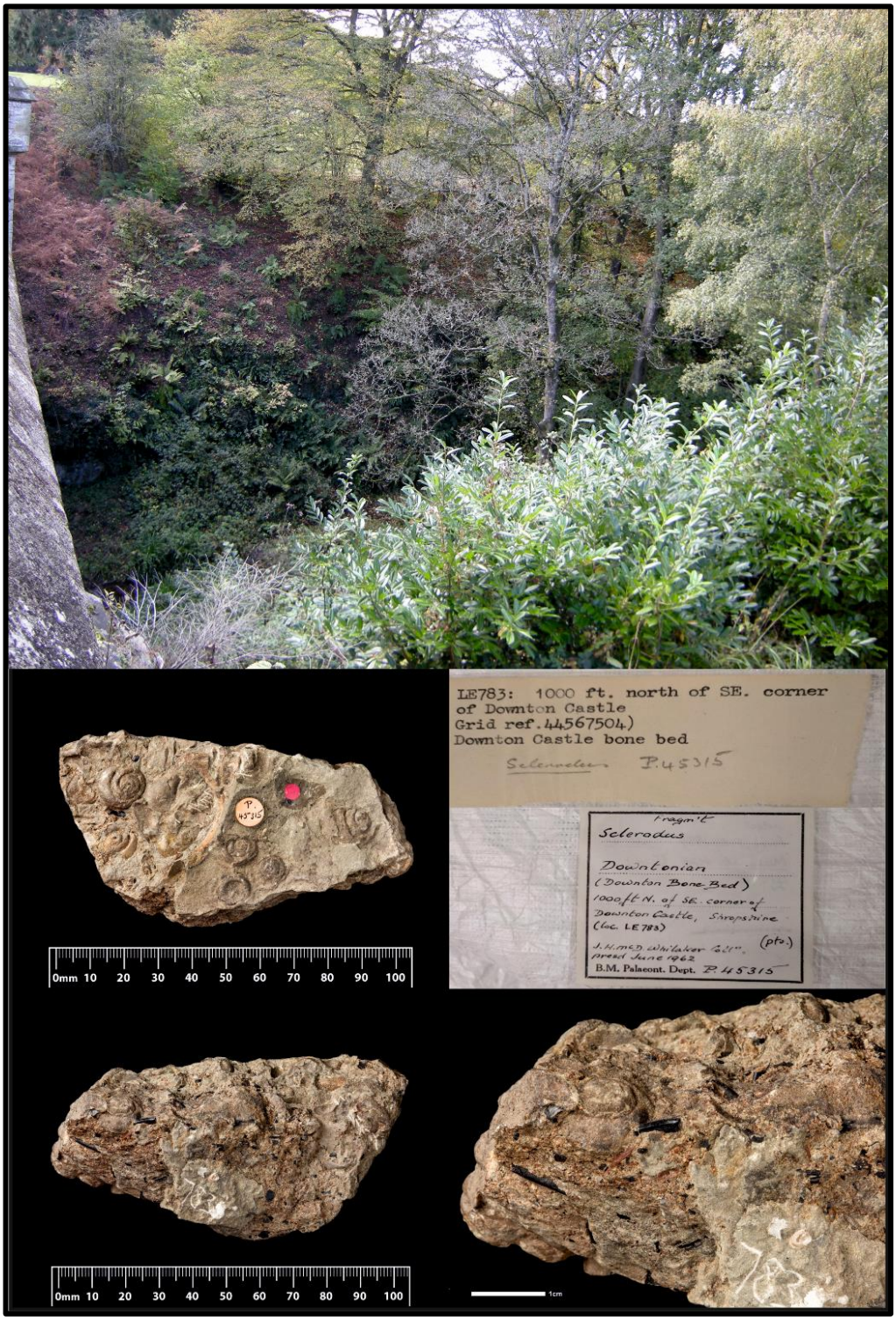
Whitaker collected a specimen (now housed in the Natural History Museum, London) from a site north of Downton Castle by the entrance to the castle (Text-fig. 3.17). The specimen matches the description of the DBB from Downton Castle Bridge given by Elles and Slater (1906) and material that they collected at Downton Castle Bridge (Text-fig. 3.14). Of interest is that Whitaker (1962) makes no mention of this site, nor does he reference the site Miller refers to as 14c. The only reference to the DBB he makes is a sentence referring to a site with excellent exposure, giving the grid reference (SO 4561 7524), which is Weir Quarry. This statement supports the suggestion that Weir Quarry was the locality showing the transition Elles and Slater described as the site of a transition into this 'bony' appearance. The inference is that Whitaker collected this sample (Text-fig. 3.17) and then referred to Weir Quarry as being a locality with good exposure of the DBB as he saw the same lithology as that of the sample he had collected. It is possible he was seeing the same lithology at Weir Quarry as he was at Downton Castle, but this has now been lost from Weir Quarry or is in another part of the quarry, unidentified.

Other locations have not been investigated due to the geographical scope of this study. The potential for further study of the DBB elsewhere is indicated by Greig et al. (1968) who stated that the DBB horizon is "recognised from Ludlow to Much Wenlock, but the characteristic gastropod is not recorded north-east of Shipton, and there, it is in the Ludlow Bone Bed". Based on the comments by Elles and Slater (1906), it is possible that Greig et al. (1968) had mistaken the DBB for the LBB and a fresh reassessment is needed.

A summary of the localities discussed in this chapter is provided in Table 3.1, indicating the state of the exposures and site details.

Localites					
	Ludford Lane	Forge Bridge	Downton Castle Bridge	Miller's locality 14.c	North of Dowton Castle 'Whitaker' locality
Grid ref.	SO 5118 7412	SO 4548 7501	SO 4447 7427	SO 4442 7402	SO 4456 7504
Site protections	SSSI	SSSI/Private land	SSSI/Private land	SSSI/Private land	SSSI/Private land
Locality access	Road	Road and track	Track	Track	Road and track
State of exposure	Poor	Poor	Poor	No longer present	unable to access to assess

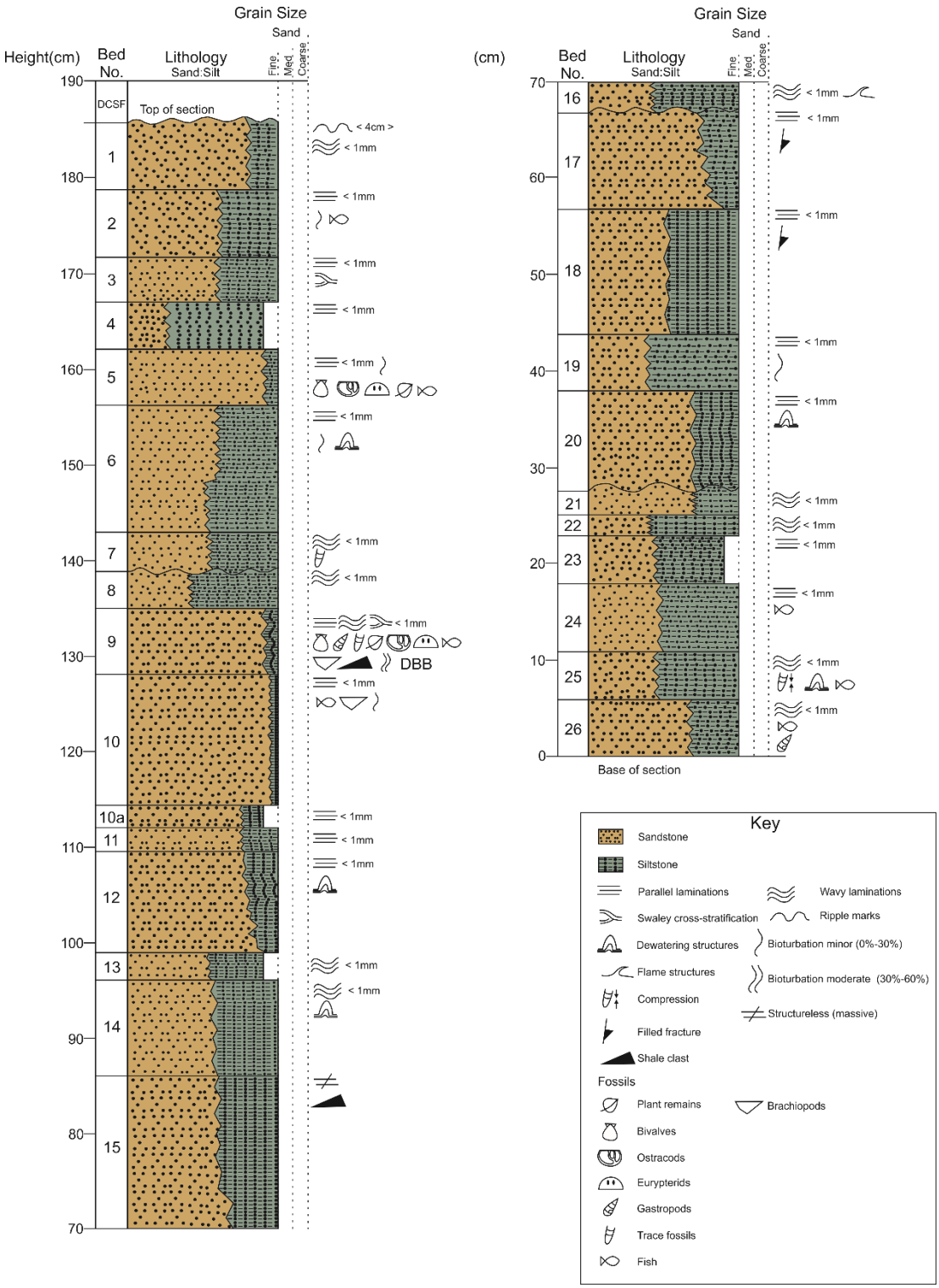
Table 3.1 Table of key localities in the Downton Gorge and Ludlow Lane area for the Downton Bone Bed.



Text figure 3.17 Whitaker locality (SO 4456 7504). The land is owned privately, and access is limited. According to the grid reference, the sample was collected from the exposure shown on the opposite bank which is now covered in vegetation. Specimen P.45315 is housed in the NHM, London.

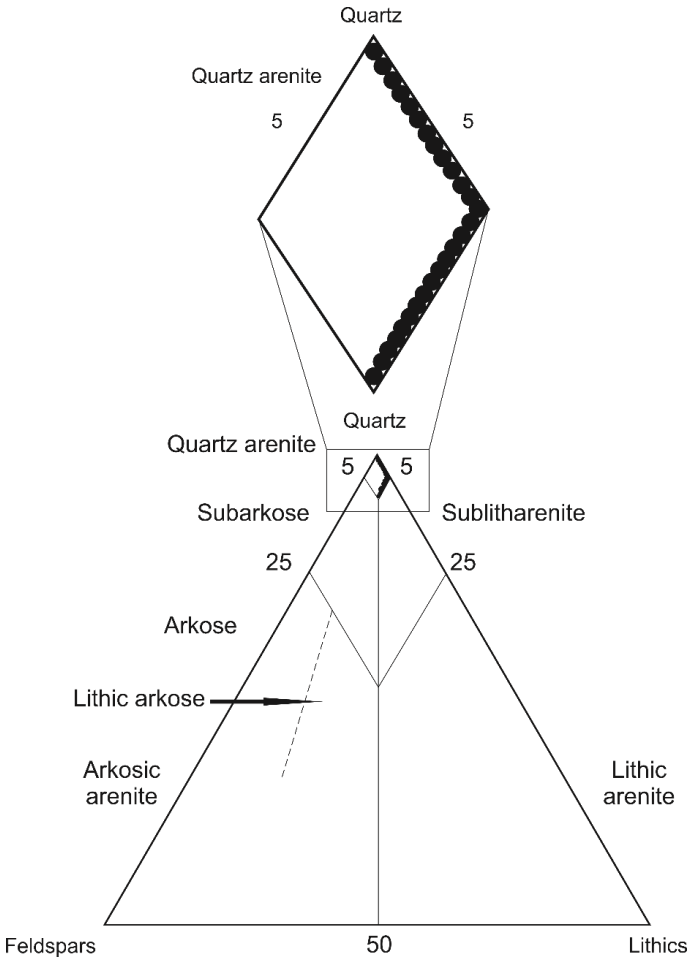
3.2 Description of the Platyschisma Shale Member at Weir Quarry

The *c*.1.87 m of vertical exposure of the Platyschisma Shale Member (PSM) at Weir Quarry comprises 26 beds (Text-fig. 3.18).



Text figure 3.18 Sedimentary log of the section through the PSM studied at Weir Quarry.

The beds are all olive to brown in colour, and all are well indurated. The grain size ranges from 0.003 mm to 40 mm, with rip-up clasts as the largest grains. The beds are interbedded fine to medium-grained micaceous sand- and siltstones. They are quartz-rich (≥ 80 % quartz) with a large amount of mica, the majority of which is muscovite with occasional biotite. No feldspars were seen in any samples and there are few lithics which, according to the Pettijohn classification, makes them quartz arenites (Text-fig. 3.19). The beds have suffered little from tectonic deformation, apart from the fault referenced in section 3.1.2. Beds 17 and 18 have vertical fractures, which are calcite-filled. Beds range in thickness from 1.5 cm to 17 cm with an average thickness of 7.6 cm. All beds show lamination, planar, quasi-planar and hummocky/swaley cross stratification which are all present throughout the member. There is infrequent bioturbation, except in bed 9 (DBB) which has horizons that are heavily bioturbated, while others show infrequent burrows. These are discussed in detail within chapter 7.



Text figure 3.19 Pettijohn diagram, plots represent beds from the PSM section at Weir Quarry.

Fossils are generally uncommon throughout the PSM section at Weir Quarry. However, beds 26, 25, 24, 10 and 2 have a few thelodont denticles (≤ 10 %). The DBB (Bed 9), however, is enriched with fossil material, not only vertebrates but also invertebrates and plants. Bed 5 also contains vertebrate fossils in a greater diversity and volume than in the other beds (excluding the DBB), but not in a comparable volume as in the DBB. Bed 5 does contain large fragments of Osteostraci, however.

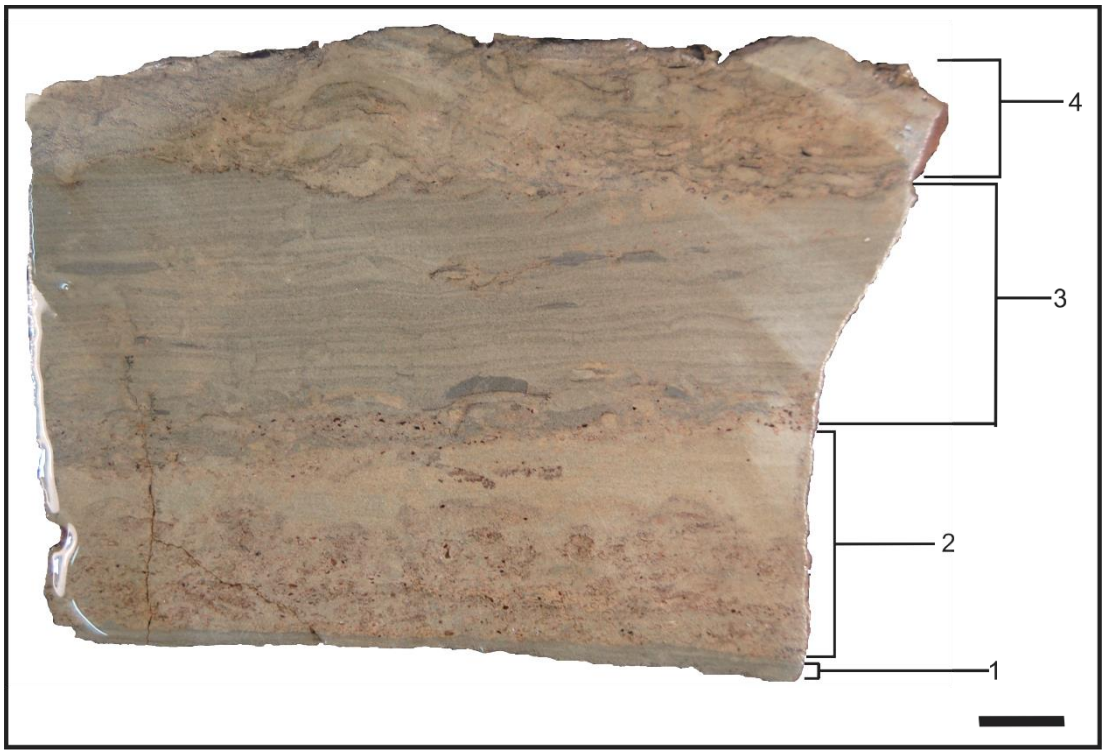
3.2.1 Downton Bone Bed description at Weir Quarry

The DBB is laterally variable in Weir Quarry. Within the c. 8 m lateral extent, 20 points were sampled (Text-fig. 3.20). These were c. 24 cm apart, and the material was collected both for extraction of fossil content and sedimentological investigation. Only two samples were missing from the hand specimens (sample points 10 and 20), because of difficulties extracting samples. What little was collected was either processed to extract the fossil content or to make thin sections.

Text figure 3.20 Weir Quarry with diagram showing points where samples were collected as well as dip and strikes.

These thin sections were used to describe the missing sample points as well as the other specimens. The description below describes the individual horizons based on thin sections (Plate 3.1) and hand specimens that make up the DBB at Weir Quarry; these can be seen across the lateral extent of the exposure. In some cases, specific horizons are better developed, and in others, some are missing (Plates 3.2-3.6).

In general, hand specimens show that the fresh surface is a mottled tan/olive while the weathered surface is brown; the rock has an irregular fracture and is well indurated. The cut sample DBBM 9, in which the DBB is very well developed, enables the bed to be divided into 4 horizons (Text-fig 3.21). However, one or more of these horizons is often missing in other cut material collected from around the DBB exposure.



Text figure 3.21 Cut section of the DBB (DBBM 9), with the four horizons (1-4) present. Horizon 3 shows quasi-planar laminations and rip up clasts. Horizon 2 shows rapid deposition of sediment. The scale bar represents 1 cm.

Horizon 1 (*c*.2 mm thick)

It is light grey, due to the higher clay content than in some of the other horizons. Planar laminations of ≤ 1 mm are present; the top of horizon 1 has an erosive surface. In thin section, the grain size of the quartz ranges from 250 µm to 375 µm. There is a substantial mica content of 30 % and a quartz content of 70 %. No denticles or other fossils are seen in this horizon, except for trace fossils. The subangular grains and well-sorted matrix indicate a moderate textural maturity. On some hand specimens, syneresis cracks are observed (Text-fig. 3.22).

Horizon 2 (*c*. 3 mm thick)

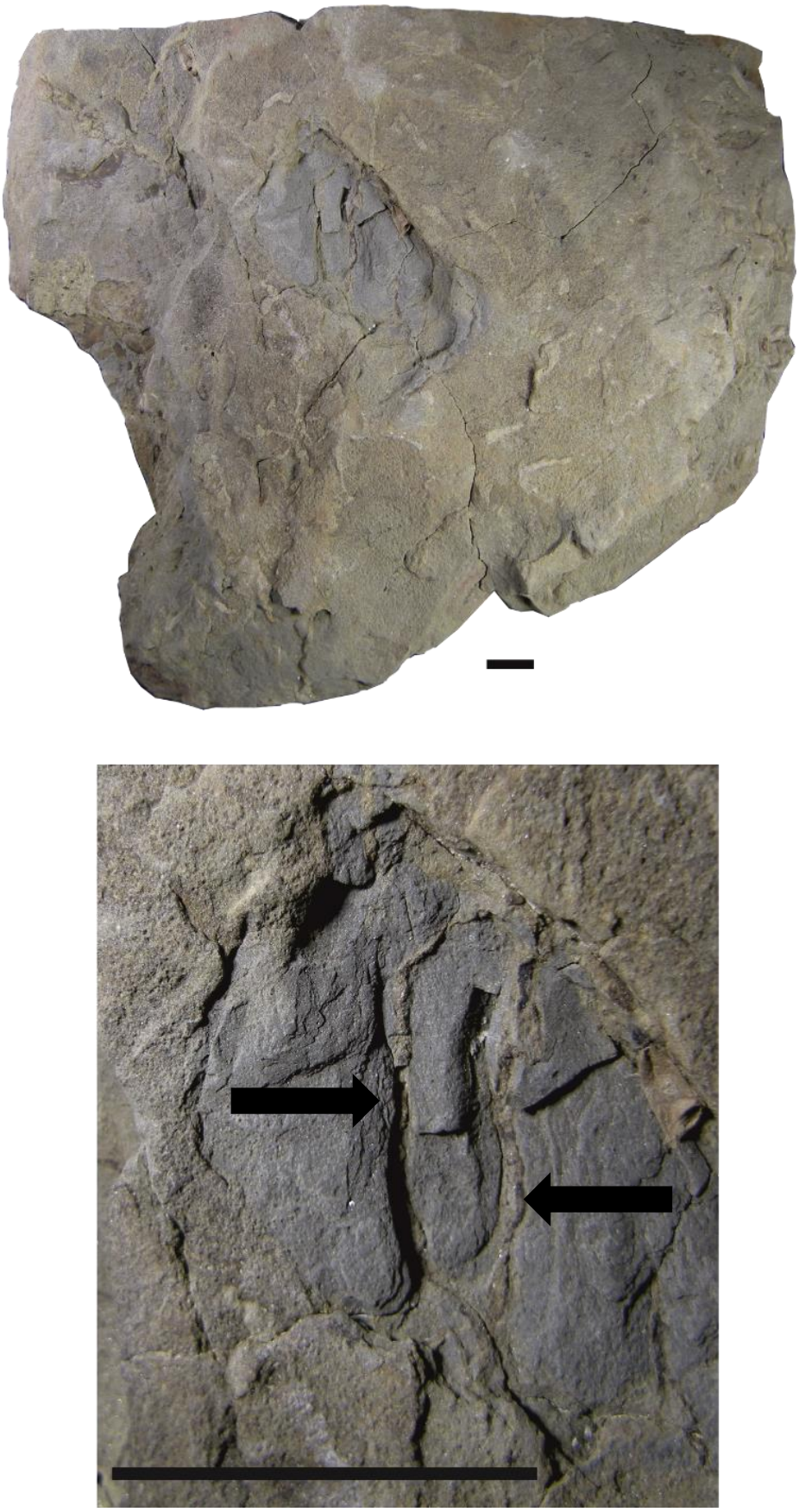
This horizon is light tan in colour, due to the reduced silt content. There are no sedimentary structures; the base and top are both erosive. In thin section (Plate 3.1, figure 2) the coarse nature of the grains can be seen; grain size is c. 700 µm. The mineralogy is 70 % quartz, 10 % micas and 20 % bioclasts. The fossil content is made up mostly of denticles, which are between 500-4000 µm and do not appear to be highly abraded, although some are broken. Ostracods are preserved as moulds with the original carapaces dissolved away. They measure between 500 µm and 1000 µm. Lingulate brachiopods are preserved as angular fragments which are between 250 and 2000 µm in size. Despite the random orientation and large size of the bioclasts, the sediment has been moderately sorted. In parts of the DBB at Weir Quarry between horizon 2 and 3, a sharp contact is observed often with an erosive boundary.

Horizon 3 (*c*. 4 mm thick)

This horizon is the same colour as horizon 1 and, as seen in the thin section, has the same higher silt content. Again, like horizon 1, there are planar laminations spaced at about ≤ 1 mm apart. The base and top of the horizon are erosion surfaces. Trace fossils are present in this horizon: *Planolites* and *Teichichnus*. This horizon also contains rip-up clasts of mudrock which range in size from 5 to 40 mm. In thin section, the grain size of the sediment can be seen to be 250-500 µm. It is well-sorted medium sand, a content of 60 % quartz, 10 % lithics and 30 % micas.

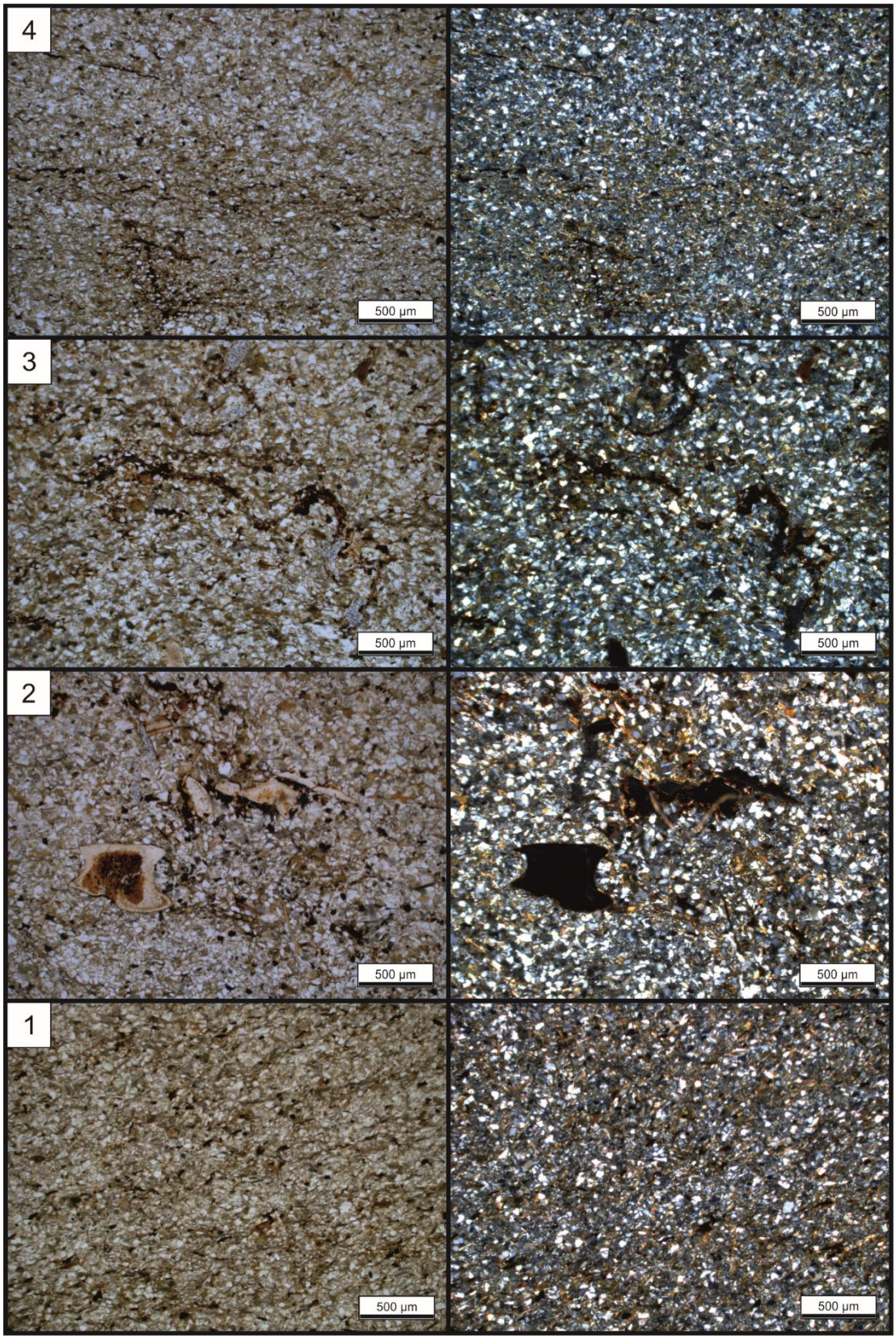
Horizon 4 (*c*.19 mm thick)

This horizon is the same light tan colour as horizon 2, and it is similarly a homogeneous sediment with a lack of sedimentary structures, again suggesting rapid deposition. There is also bioturbation present. Horizon 4 has an erosive base. In thin section, the similarities with horizon 2 continue as the grain size is 375 μm to 750 μm. It is coarse sand; the sorting is moderate due to the bioclasts. The horizon is made up of 70 % quartz, 10 % micas and 20 % bioclasts. The bioclasts are at random orientations and consist mostly of denticles ranging in size from 1000-4000 μm.



Text figure 3.22 Example of syneresis cracks (arrows) seen in the DBB on horizon 1 from sample DBBM 5. Scale represents 1 cm.

Plate 3.1



Explanation of Plate 3.1

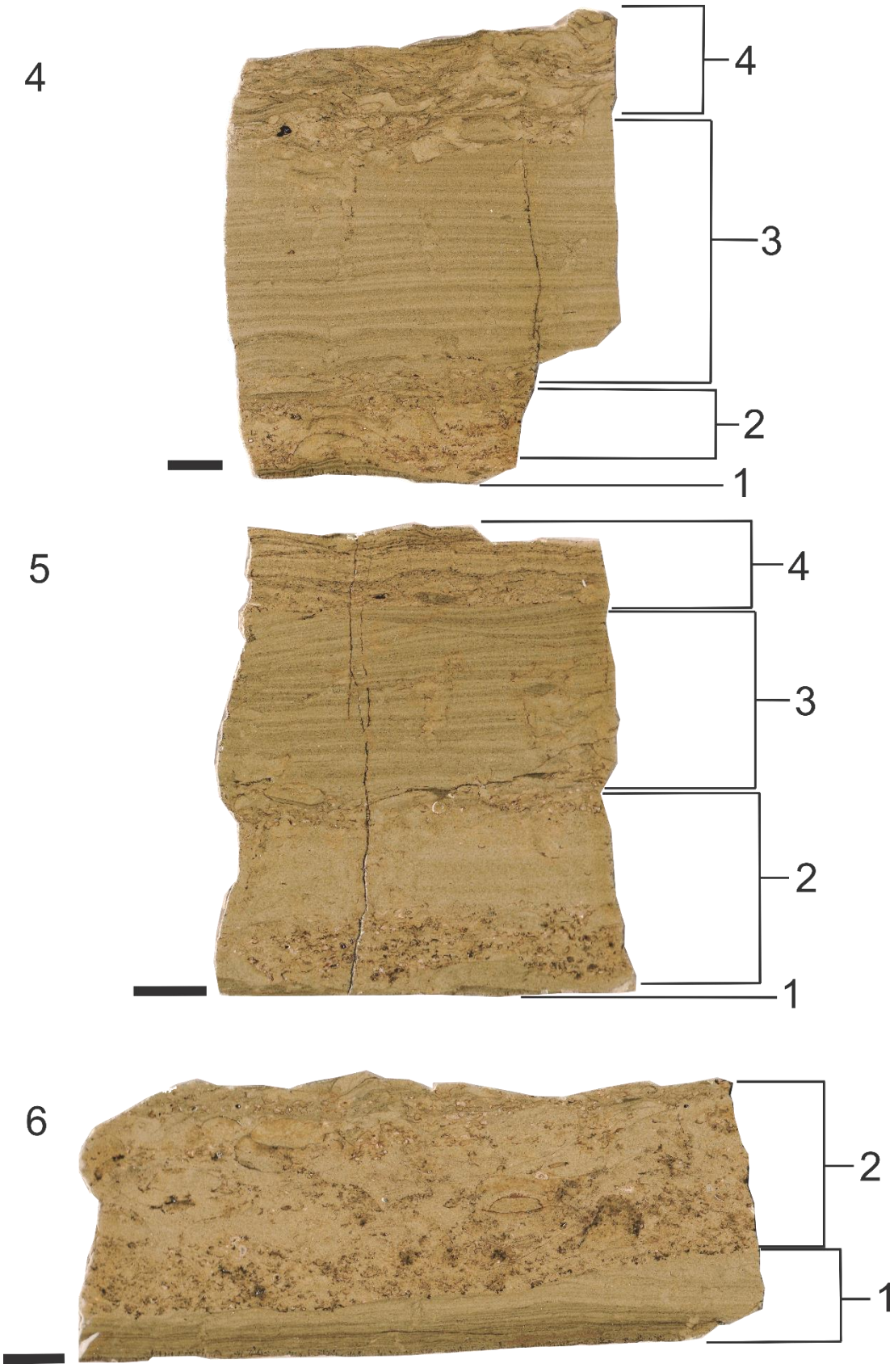
Thin sections of each horizon (1-4) of the Downton Bone Bed in stratigraphical order; left-hand side is in PPL (Plain Polarized Light) and right is in XPL (Crossed Polarized Light).

Plate 3.2

Explanation of Plate 3.2

Cut sections of DBB at Weir Quarry, samples from collection points 1-3. 1) Swaley cross stratification present with well-defined laminations, but no fossils present. 2) Has all four horizons with the bone bed being deposited in between horizons 1 and 2; 2 and 3; 3 and 4. Horizon 3 shows the typical planar laminations, while horizon 4 has wavy laminations. 3) dominated by horizon 2, with wavy laminations. The fossils are deposited on the top of horizon 2. Scales represent 1cm.

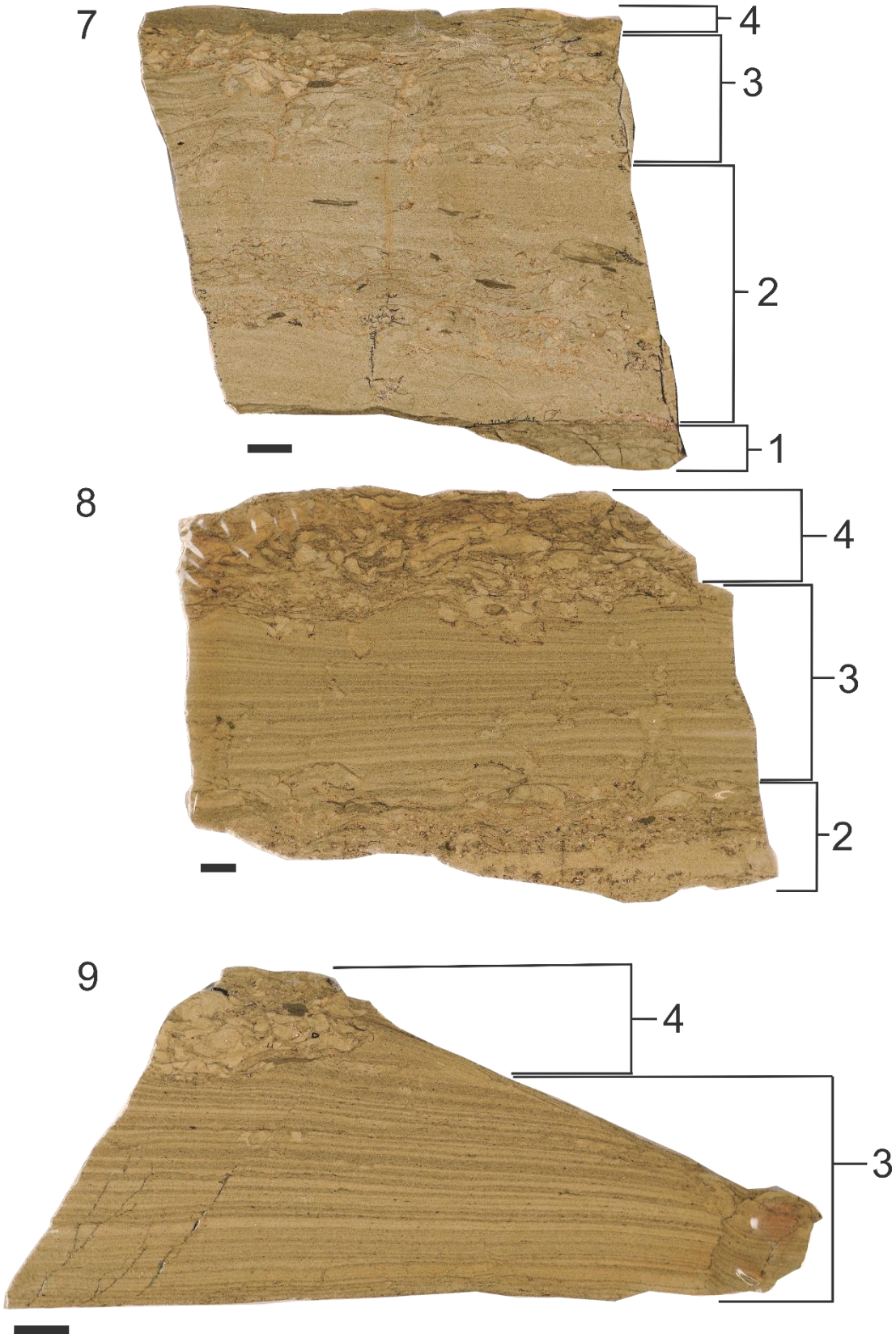
Plate 3.3



Explanation of Plate 3.3

Cut sections of DBB at Weir Quarry, samples from collection points 4-6. 4) all four horizons are present, although horizon 1 is very thin. The thickest horizon is horizon 3 which again shows planar laminations, the laminations that were present in 4 have been lost to bioturbation while fossils are mostly confined to horizon 2. 5) The four horizons are still present; however, horizon 1 is now very thin. Horizon 2 still contains many fossils, while horizon 3 has planar laminations with swaley cross beds at the top. 6) At this point horizons 3 and 4 are missing while horizon 1 has increased in thickness and displays planar laminations, horizon 2 has an erosive base, the horizon is full of fossils. There are several cross-sections of the gastropod *Turbocheilus helicites*. Scales represent 1 cm.

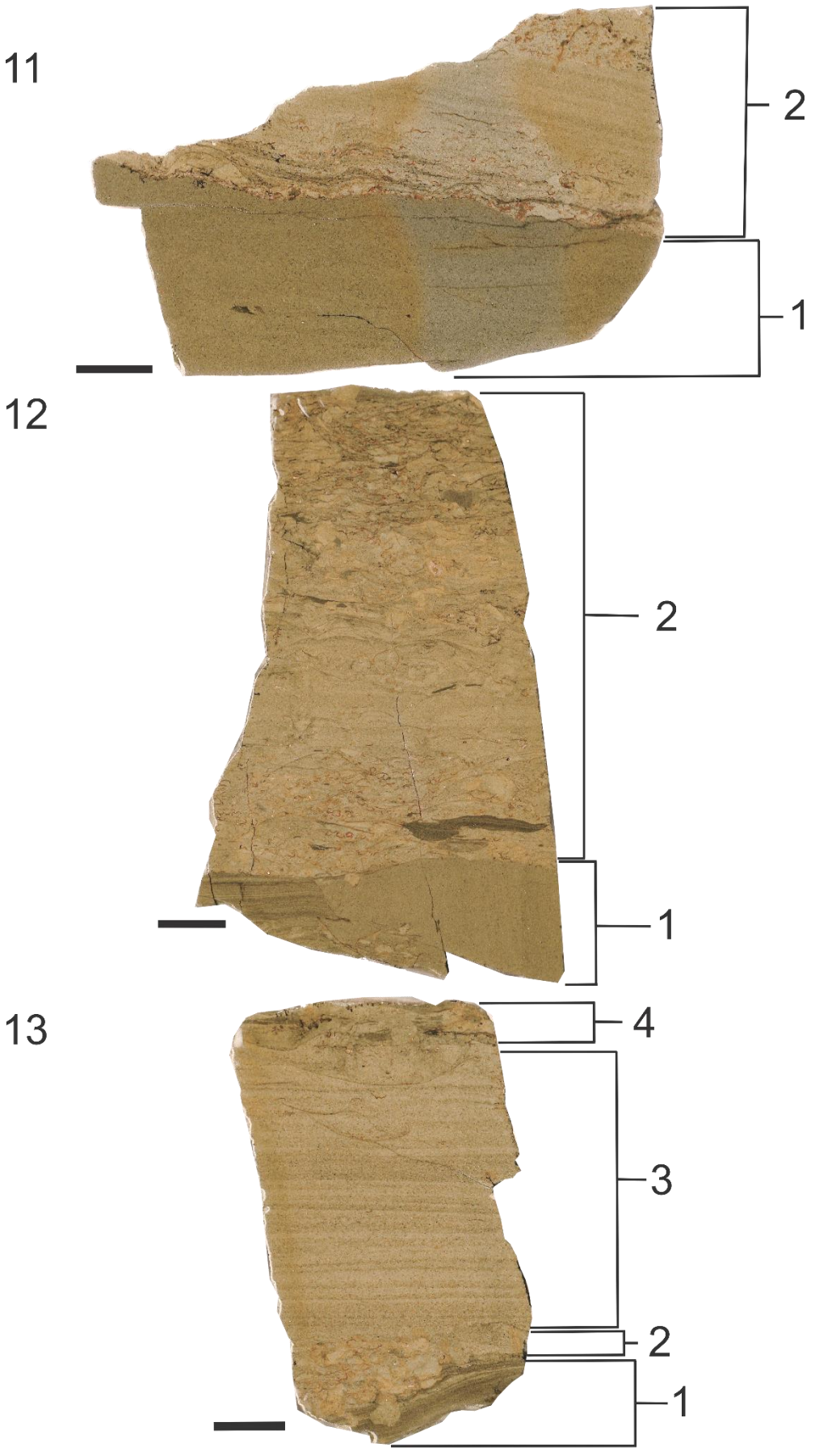
Plate 3.4



Explanation of Plate 3.4

Cut sections of DBB at Weir Quarry, samples from collection points 7-9. 7) The four horizons are now present. Horizon 1 has thinned out, and at the interface between horizons 1 and 2 a significant amount of vertebrate material is present. 8) This is an incomplete bed as can be seen by the irregular lower surface, this, however, is the best example of sample point 8 in the material collected from Weir Quarry. Horizon 2 would likely continue down, though it is unclear if horizon 1 would be present. 9) Only the upper two horizons are present; the bed is dominated by horizon 3, which shows planar laminations. Scales represent 1 cm.

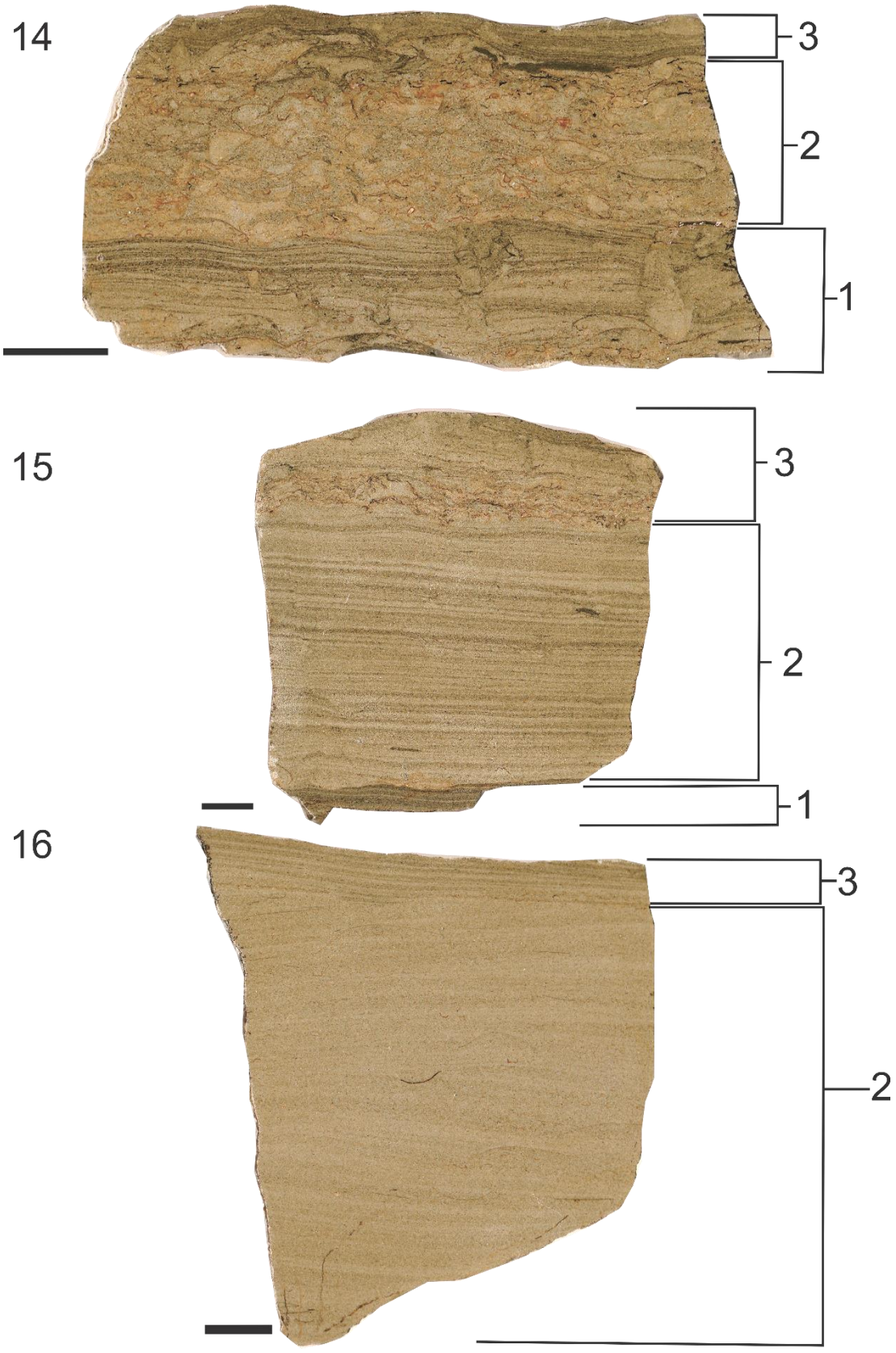
Plate 3.5



Explanation of Plate 3.5

Cut sections of DBB at Weir Quarry, samples from collection points 11-13. 11) Is an incomplete bed, the upper horizons 3-4 are not present. Horizon 1 is homogeneous silt, while horizon 2 has an angled erosive base and represents a sharp change in sedimentary input. At the boundary between horizons 1 and 2, vertebrate fossils are seen. Horizon 2 has planar laminae. 12) Continues to show only the lower 2 horizons although the thickness of the bed has greatly increased, horizon 1 is still homogeneous silt with a planar laminated rip-up clast in the lower left-hand side. Horizon 2 also shows a mud rip-up clast in the lower section. However, there are few laminations with the rest of the horizon, as it looks as if bioturbation has taken place near the top of the bed. 13) The four horizons return, and the overall thickness of the bed decreases. Horizons 1 and 2 are very thin and horizon 2 has an erosive base once again. Horizon 3 displays more planar laminations and is the thickest horizon. Horizon 4, like horizons 1 and 2, is very thin. Only a few vertebrate fossils are seen at the interface between horizon 3 and 4. Scales represent 1 cm.

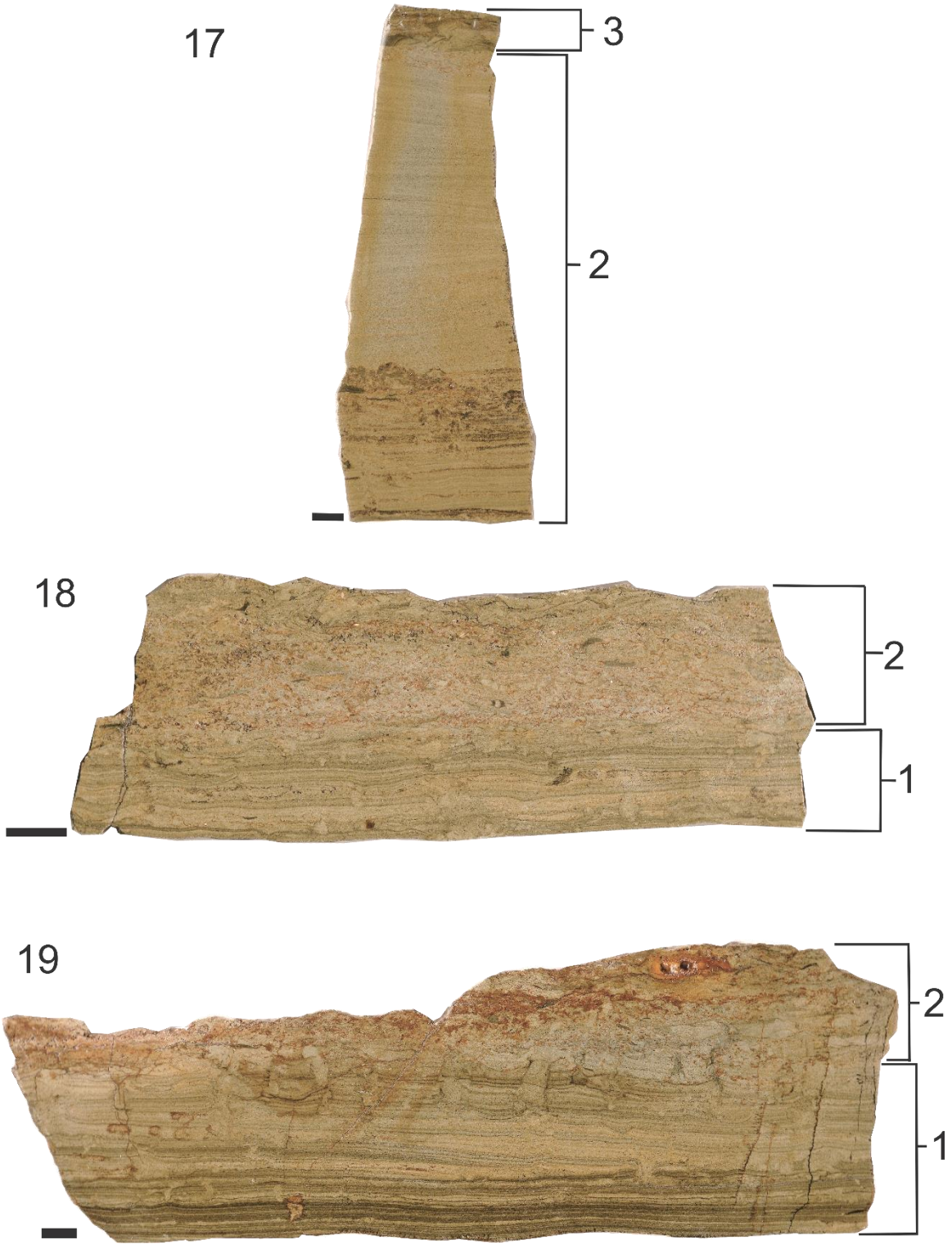
Plate 3.6



Explanation of Plate 3.6

Cut sections of DBB at Weir Quarry, samples from collection points 14-16. 14) Horizon 4 is absent at point 14. However, horizon 1 has increased in thickness and shows planar lamination as well as numerous trace fossils, while horizon 2 is bioturbated with oxidised material (likely shell fragments). This horizon contains all of the fossils preserved in this sample. Horizon 3 has a reduced in thickness and has more silt than is common in this horizon. Quasi-planar laminations are present. 15) The bed is thin and is missing the fourth horizon. Horizon 2 has an erosive base, and the fossil material is aggregated at the interface between horizon 1 and 2. Horizon 2 is consistent with planar laminations. 16) Is a generally featureless bed with only two horizons, horizon 3 does have planar laminations. Scales represent 1 cm.

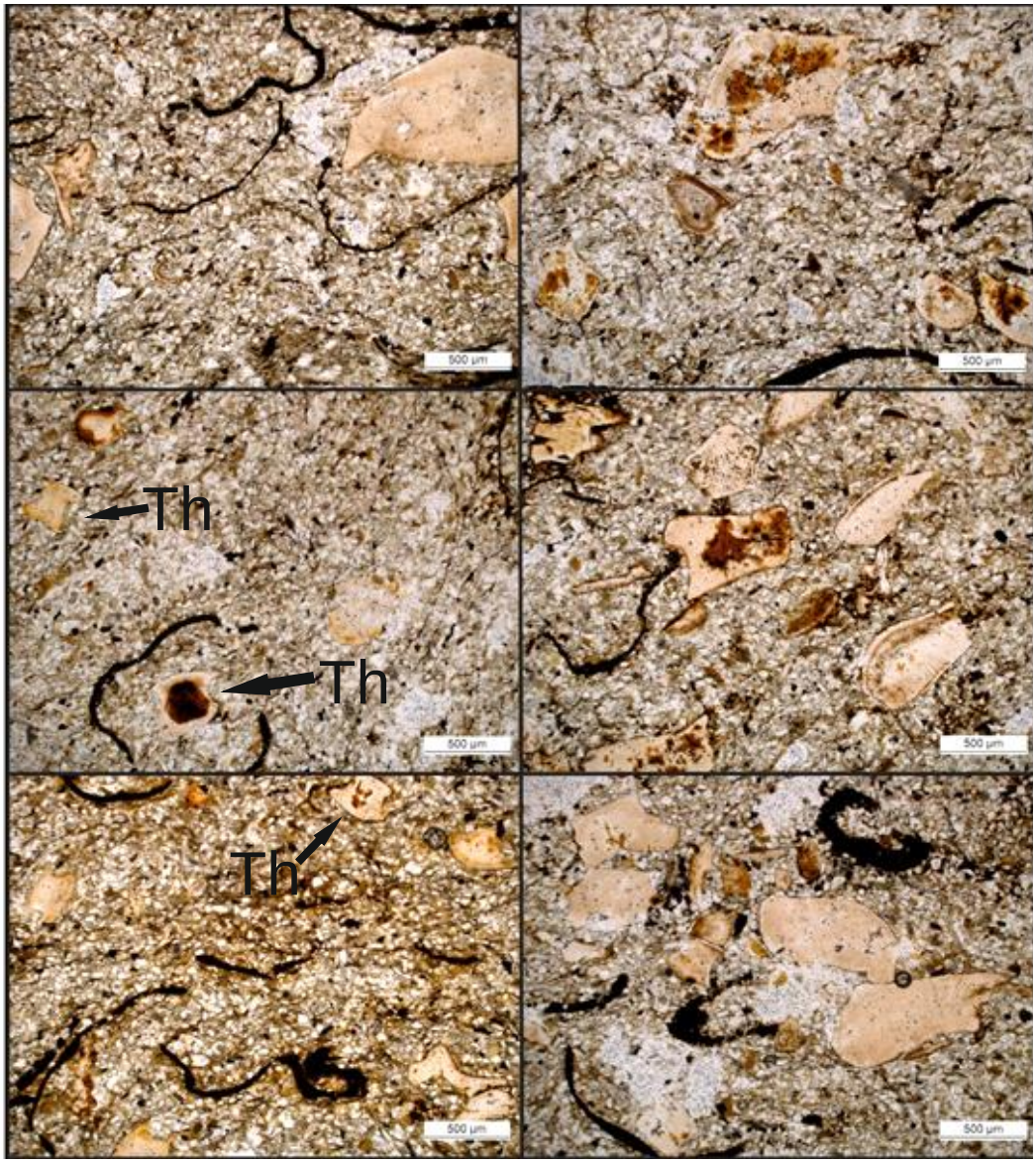
Plate 3.7



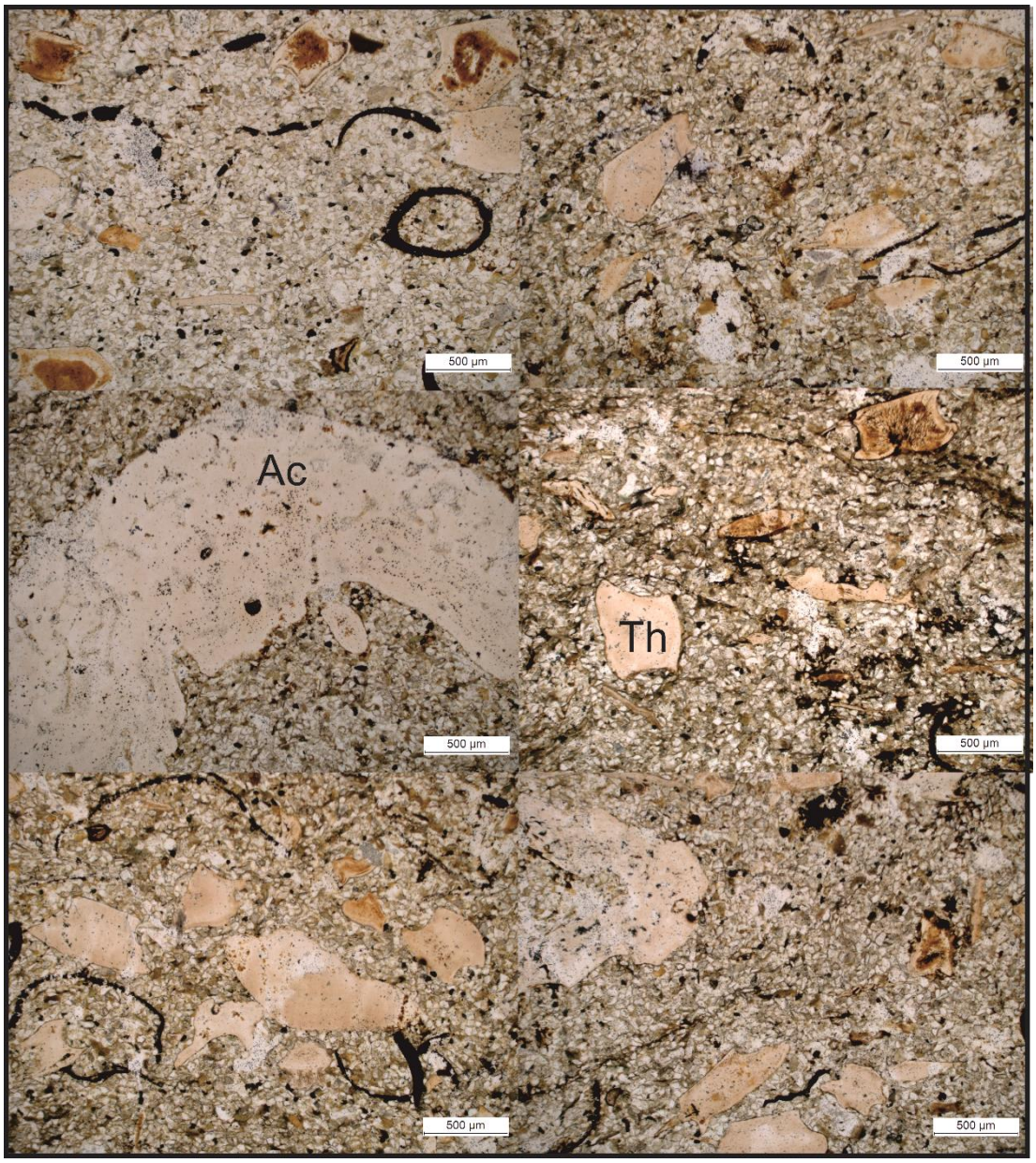
Explanation of Plate 3.7

Cut sections of DBB at Weir Quarry, samples from collection points 17-19. 17) The bed thickness has once again increased and only horizons 2 and 3 are present. At the interface between 2 and 3 fossils are present. 18) The bed has thinned; only horizons 1 and 2 are present. Horizon 1 has planar laminations as well as many trace fossils, while horizon 2 is structureless and has oxidised material mixed in with vertebrate material. 19) The bed is similar from the last sample point as only horizons 2 and 3 are present. However, horizon 1 has become thicker and is even more bioturbated than 18. Finally, horizon 2 is rich in fossil material but is structureless. Scales represent 1 cm.

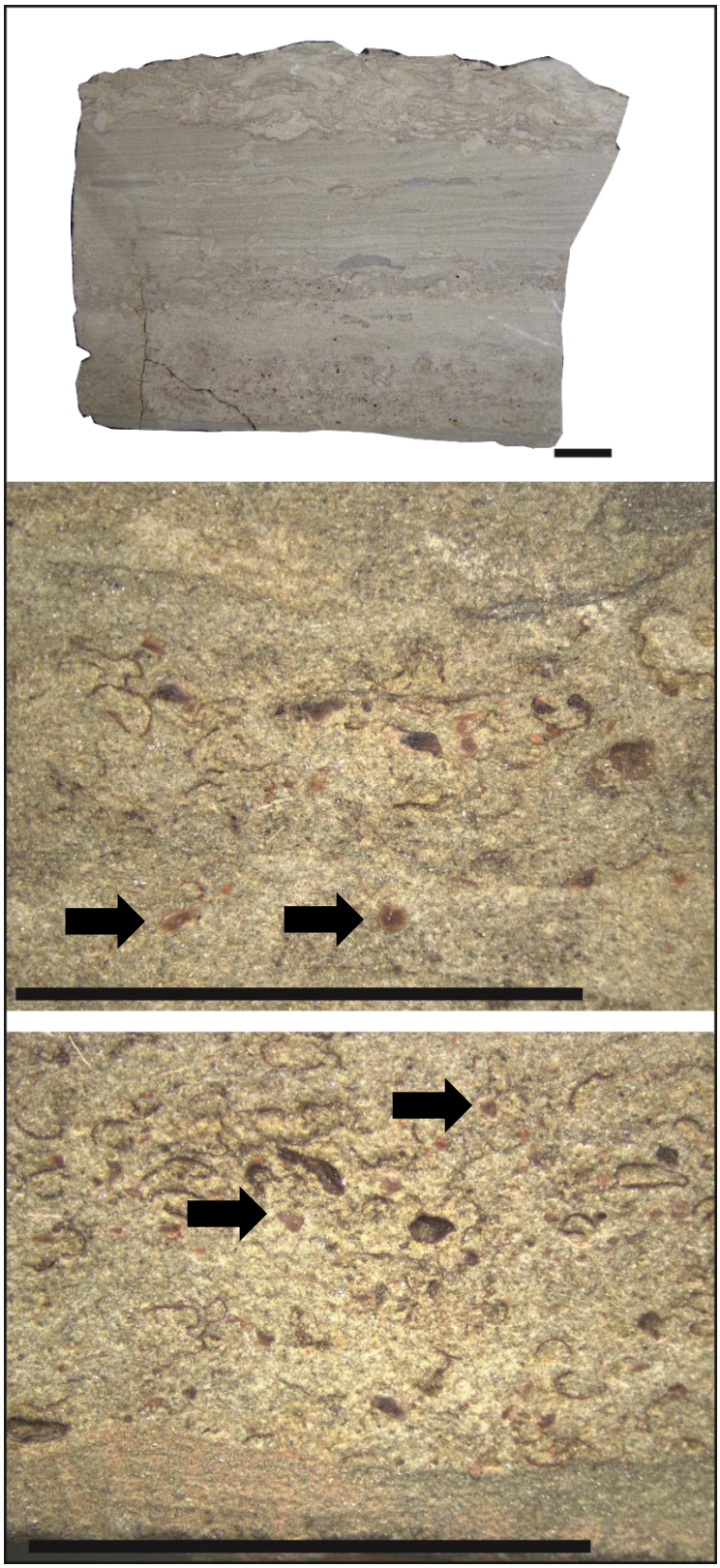
The bonebed itself at Weir Quarry is diffuse when compared to the bonebed at the Downton Castle Bridge localities (Text-figs. 3.15 and 3.17), but Text-fig 3.23 and 3.24 show that across the lateral extent of the exposure there are many denticles present in the bed. These are often not obvious in hand specimen (Text-fig. 3 25) because the colour of the denticles is lighter (less reworked) than is seen at Downton Castle and what was described from Linley Brook (Bradfield and Tucker 1986).



Text figure 3.23 Examples of the Downton Bone Bed from Weir Quarry; sample points 5 and 6 illustrating the richness of the bonebed; thelodont (Th) denticles are visible in these thin sections.



Text figure 3.24 Examples of the Downton Bone Bed from Weir Quarry; sample points 7 and 6 illustrating the richness of the bonebed; including thelodont denticles (Th) and an acanthodian spine (Ac).



Text figure 3.25 DBBM 9 with two close-ups showing how inconspicuous some of the vertebrate fossils (arrows) are within the bed, illustrating that they can easily be overlooked.

3.3 Facies interpretation

When considering the sedimentology of the DBB, it is important to state that previous studies concerning the DCSF (that contains the DBB) have focused on large-scale geology. The authors often have studied the formation as a whole when making interpretations. The challenge in this study is that one site was intensely studied, and now a complete image must be produced which fits into the established literature. Because this study focused on one locality (Weir Quarry), it is not possible to make conclusions on the depositional setting of the DBB as a whole, only what is exposed at Weir Quarry. Additionally, unlike the LBB which is consistent in appearance across its known range, the DBB changes markedly across only 7 km, and even within Weir Quarry, going from diffuse to very rich. To address this problem, many of the key localities that Elles and Slater (who first established the DBB) were visited so that the sedimentology could also be studied. The other principal aim of this section and study is to establish how the DBB formed within the PSM.

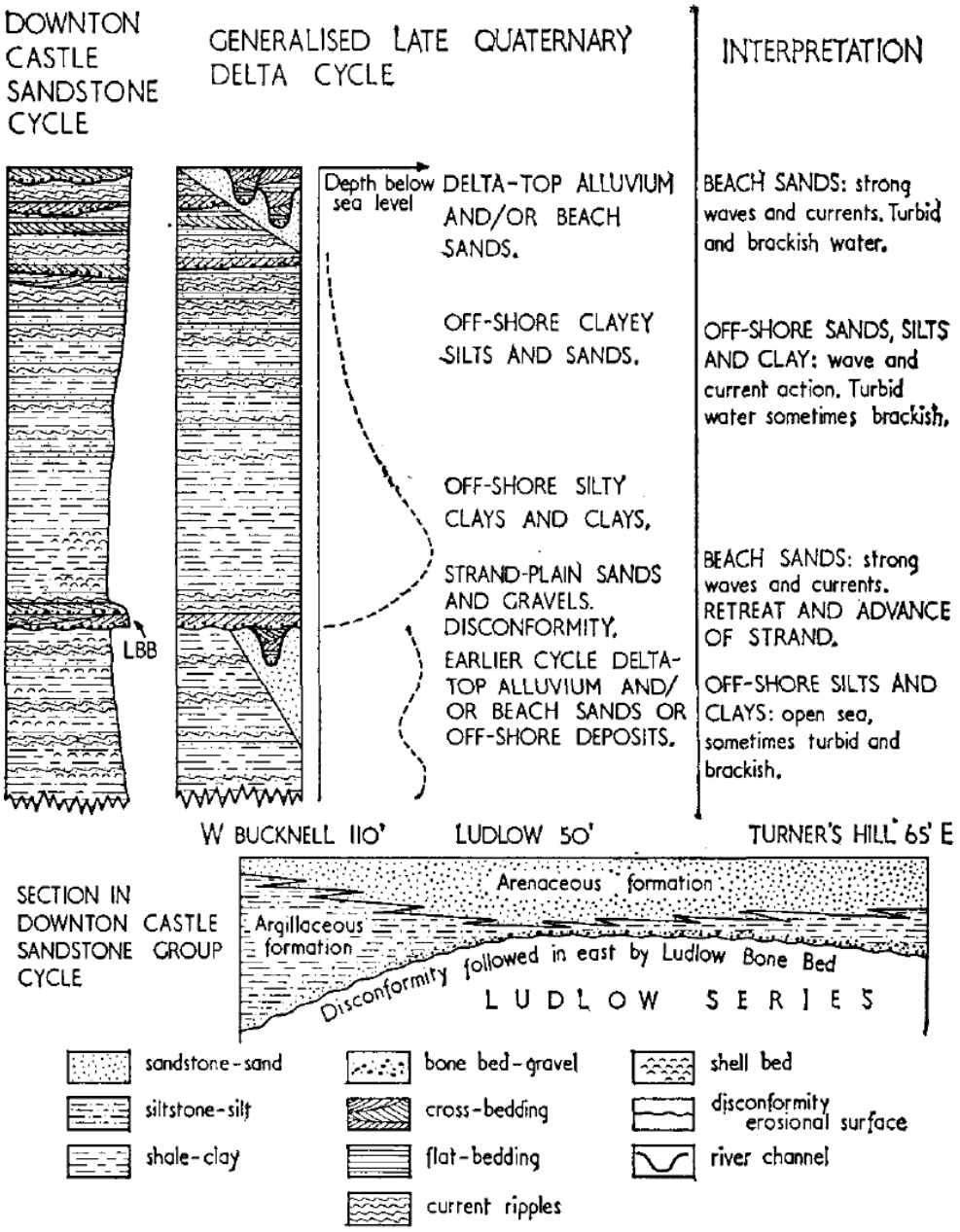
Using the description of the DBB from Weir Quarry, it is then possible to look at previous literature on the PSM and the DCSF and determine whether any similarities can be observed with what is seen at Weir Quarry.

Allen and Tarlo (1963) described the Downton Castle Sandstone Group, which is equivalent to the DCSF. Due to the fact that they described the LBB separate from the Downton Castle Sandstone Group, there is confusion when they state that the lower beds of the Downton Castle Sandstone Group resemble that of the uppermost of the Ludlow Series. This name would in modern nomenclature refer to the UWF, which is not similar to the PSM; they also refer to bonebeds being present in the Ludlow Series. This was before the DCSF was established, with the LBB as the base of the formation. As the nomenclature is different, some interpretation is needed to clarify which sections refer to the lithology seen in this study. Various localities were looked at including Ludlow, Much Wenlock, Clun Forest, Long Mountain, Turner's Hill, Nertheron, Lye, Woolhope, May Hill, Usk, Cardiff, Malvern and the Abberley hills. The description of what would now be considered to be the PSM is as follows: "The argillaceous rocks grade up into thick yellow, well-sorted fine sandstones, crowded locally with *Lingula*, and the sedimentary structures include flat-bedding,

current-bedding, scour-and-fill, current ripple-marks and graded-bedding. Eroded contacts between sandstones are common and are often marked by uneven scoured surfaces, succeeded by thin intraformational conglomerates or pebbly layers of siltstone pebbles, shell debris, and vertebrate remains. These remains include fragments of acanthodians and thelodonts as well as *Sclerodus*, *Cyathaspis*, and the cephalaspids *Thyestes* and more rarely *Hemicyclaspis*, a fully articulated specimen of which was recorded from Turner's Hill (Wills, 1948, Ball, 1951)". This description does mention several sedimentological features seen at Weir Quarry; the well-sorted fine sandstones, crowded locally with *Lingula* is not dissimilar to what is seen within the DBB with the bonebed containing the brachiopod *Lingula*. Many of the structures are also recorded at Weir Quarry such as the flat bedding and erosive contacts. Allen and Tarlo (1963) also described the intraformational conglomerates that contain shell debris, and vertebrate remains, and while initially, this would seem to describe the DBB they go on to describe them also as pebbly layers of siltstone pebbles. This is not seen in the DBB at Weir Quarry. However, after this Allen and Tarlo (1963) described, "Occasional beds of siltstone are intercalated with the sandstones and these yield *Modiolopsis* as well as ostracods, gastropods, eurypterids, and fragments of vertebrates". This is similar to what is described at Weir Quarry, the alternating sand- and siltstones, which contain all of the fossils.

The fossil content will be discussed within the relevant chapters; however, it should be noted that these fossils (recorded by Allen and Tarlo 1963 and others), along with the sedimentology, are similar to what is seen at Weir Quarry. As such, a description emerges of a thick yellow fine well-sorted sandstone with beds with erosive bases and flat, current, scour, and fill structures with occasional beds of siltstones intercalated with sandstones that contain numerous fossils. The interpretation that Allen and Tarlo (1963) suggested for the Downton Castle Sandstone Group is cyclic deposition such as on modern deltas e.g. the Quaternary of the Mississippi Delta (Text-fig 3.26) (Fisk et al. 1954). They suggested that the DCSF was deposited during a transgressive cycle and records a period when the strandline retreated across the Welsh Borderlands. Furthermore, the beach and offshore sands were spread over deeper waters silts of the turbid and brackish waters of the Downton Sea, which had been introduced by the earlier transgression. Allen and Tarlo also mentioned that the

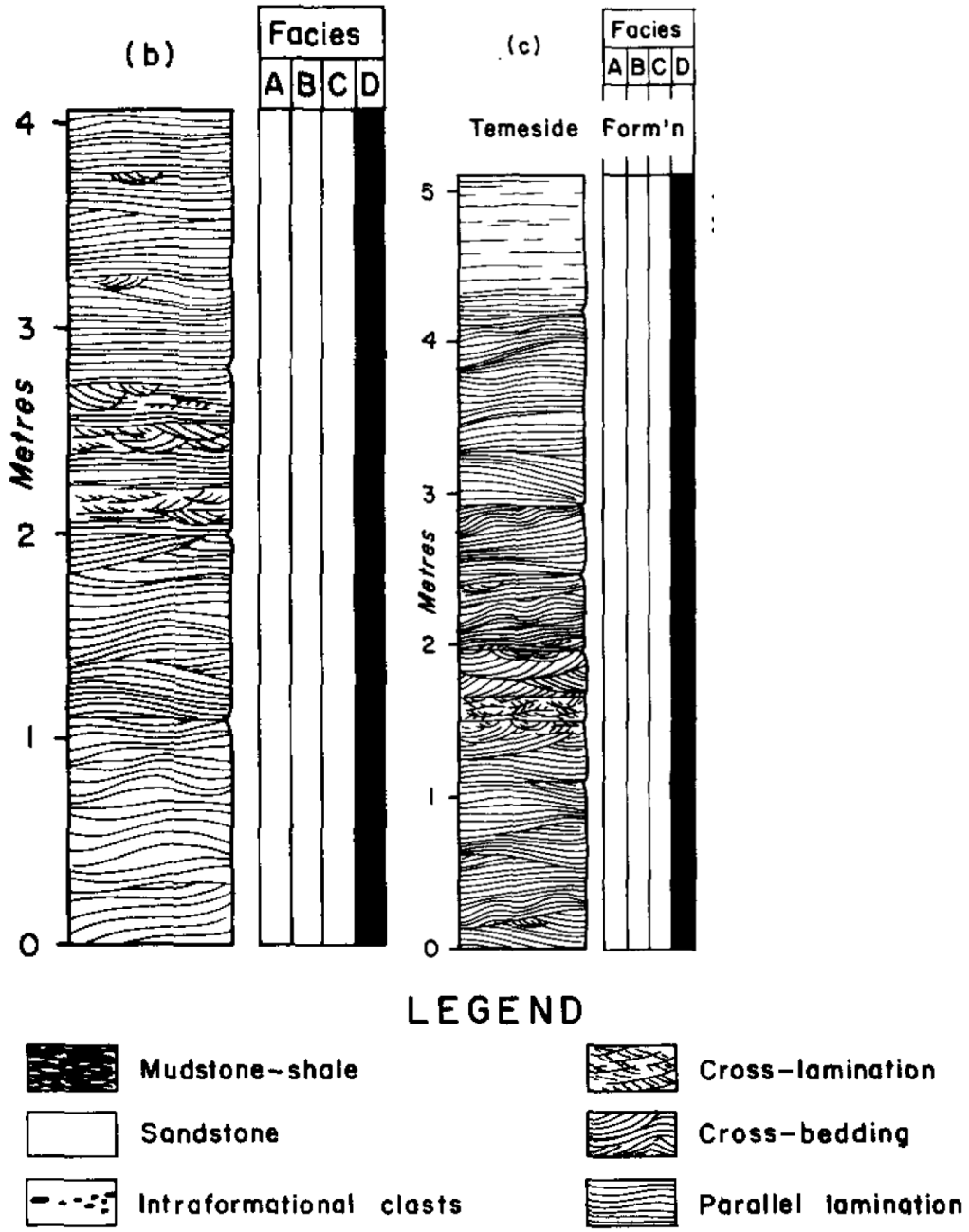
invertebrates that are recorded within the DBB flourished under shallow water conditions.



Text figure 3.26 Allen and Tarlo's (1963) text figure 2 of the Downton Castle Sandstone Group and their interpretation.

This interpretation is functional and could fit with some of the evidence gathered from Weir Quarry; however with further work having been carried out and with different depositional interpretations, it is necessary to consider other researcher's interpretations before committing to any one setting.

Later Allen (1974) divided the DCF into 4 facies: Facies A is the LBB and therefore will not be considered any further in establishing which facies fits closely with the PSM section at Weir Quarry. It is likely to be Facies B that is representative of what is recorded in this study from Weir Quarry. Facies B represents 1-2 m of strata that contains several features such as parallel laminations, erosive bases and the presence of bone sands.



Text figure 3.27 Logs modified from Allen's (1974) fig. 21 of sections taken from two localities, of significance to this study; (b) upper part of the formation, quarry near Downton Castle (SO 447750) and (c) upper part of formation, quarry near Downton Castle (SO 455751).

This facies would likely cover the PSM, and by reference to Allen (1974) fig. 21; (Text-fig. 3.27), the choice of facies can be further narrowed down. The two sections shown in Text-fig. 3.24 are both from the Downton Castle area: (b) was c. 150 m southeast of the locality where Whitaker collected the DBB sample (SO 4456 7504) while (c), was c. 165 m southwest of Weir Quarry and shows the base of the

Temeside Formation. This section would likely correspond with the Sandstone Member of the DCSF. If this is the case, then Facies D can be ruled out as the facies that represents the strata containing the DBB. This would also allow Facies C to be discounted as if Facies D represents part of the Sandstone Member that would make Facies C the highest part of the PSM above the level of DBB.

Facies B includes shell-strewn erosional bases, as well as parallel laminations overlain by cross laminations. Crucially, description of Facies B includes mention that "streaks of bone sand can generally be found within the mudstones". This is interpreted as referring to the DBB, remembering that Elles and Slater (1906) described the DBB as being diffuse in appearance before transitioning into a full "bonebed". It is suggested that Facies B is the closest match to the PSM of Weir Quarry, although caution is required as Allen's (1974) interpretations are based on a generalised model based on various localities across the Clee Hills area. The depositional environmental model suggested by Allen (1974) is that the DCF accumulated in a marine-influenced, if not a fully marine environment. Evidence for this comes from the fossils that he records; he suggests that the restricted fauna and local plant concentrations are evidence that it was close to land in turbid waters. The comparison is made to vertical patterns of regressive facies sequences, which are found today on sandy accretionary coasts, due to the Downton Castle Formation representing a coarsening-upwards "sand" body (Allen and Tarlo 1963; Allen 1974). It is suggested that the analogues for the upward sequence of interbedded mudstone, siltstones and sandstones of Facies B, which are then followed by the thick well-sorted sandstones recorded from Facies D which is recorded in vertical facies profiles in the Downton Castle Formation (his fig. 21). This is represented by the interbedded shoreface deposits succeeded by beach sands of the east coast of the North Sea, the Niger Delta, the northwest Gulf of Mexico, the Rhone delta and the barrier islands of the eastern U.S.A (Allen 1974). Ultimately, the strata were felt to represent a tidal inlet with barrier islands.

Development of the two previous interpretations continued as Antia (1980) described the sediments from the "Ludlow-Downton" boundary (later Přídolí). The conclusion that he came to is that the strata represented a tidal mudflat. To support his model, he highlighted the presence of lenticular bedding and mud cracks. Despite this, no

evidence (such as desiccation cracks) has been found within this study to support a depositional environment of a tidal mud flat.

Bassett et al. (1982) put the case forward for the Downton to be regarded as the fourth series of the Silurian System. This was not agreed upon as the Přídolí is now recognised as the fourth series in the Silurian System. The summary they give for the depositional setting of the PSM: "The Platyschisma Shale Member comprises up to 2 m of olive mudstones and siltstones, often laminated and with streaks of 'bone' sand and wavy bedding. Shelly marine faunas are present in bands, characteristically as associations of gastropods and bivalves, together with ostracods, eurypterids, and plant fragments; these fossils indicate the persistence of marine deposition, which is considered to have been in an intertidal environment off prograding sandy shores". The streaks of bone that they refer to are most likely within the '*Platyschisma* Bed' (E*b*) of Elles and Slater (1906) which passes laterally into the DBB. Their model suggests that the PSM is a tide-dominated environment; however, as previously stated, there is little evidence (such as herringbone cross bedding) for this in the PSM at Weir Quarry.

Smith and Anisworth (1989) looked at the same section from which Antia (1980) and Bassett et al. (1982) described the DCSF at Ludford Corner. They referred back to Allen (1974) whose interpretation of the depositional setting was that it represented a tide-dominated inlet fill and they agreed with Antia (1980) who proposed a tidal mud flat interpretation. The crucial observation that Smith and Ainsworth (1989) make within their paper is that of hummocky cross-stratification. This is vital as it's the first evidence the environment being storm dominated rather than tide dominated. In addition, Smith and Ainsworth (1989) mention the presence of skeletal sands, described as being the result of storm reworking during a period of low sediment supply. It is further added that some of the features that Antia (1980) had observed to support his tidal regime could not be found, such as herringbone cross stratification, trough cross-bedding and that the mud cracks were misidentified syneresis cracks, which were also observed by Smith and Ainsworth (1989). With this new data, a new model for the depositional environment was suggested. The Smith and Ainsworth model uses the very shallow (< 2 m) storm dominated shoreface of Lake Huron (North America) as an analogue. They also suggest that

size of Lake Huron (c. 60,000 sq. km) is comparable to that of the Downton Sea. It is added that the syneresis cracks are evidence of changes in salinity.

Looking at the previous 5 key papers which are most relevant to this study, and which over the decades have looked at the strata of the Welsh Borders, and in particular the area that is relevant to this study, a couple of themes appear: first, that the DCSF represents a shallow marine deposit, and second, that it is a restricted environment. The more significant shift in the last 30 years of research is from interpretation as a tide-dominated environment, which persisted from at least the 1960s, to a storm-dominated environment.

Evidence for the section representing a tide-dominated environment is that the background sedimentation is represented by alternating laminations of sand and silt, and this could be evidence for differences in tidal energy (sand was deposited with a strong tide and the silt on a slack tide). Unfortunately, this is the only evidence that could represent tidal deposition, and as will be shown, evidence for a storm-dominated deposit is far stronger.

The primary line of evidence from the Weir Quarry section for a storm-dominated environment comes from the DBB itself. As discussed earlier, the DBB includes horizon 2 which appears to have been formed through a high energy event as is evidenced from the base having an erosive contact with horizon 1. Such erosive bases are often an indication that the sediment was deposited during storms (Reading 2009). Another line of evidence for this being storm deposit is the fact that horizon 2 often fines upwards, indicating that as the energy levels returned to the background conditions, fine-grained sand settled out of suspension. The sedimentary structures seen in the Weir Quarry section also support a storm-dominated environmental setting interpretation, as there are numerous examples of hummocky or swaley cross stratification which is typically associated with storm influenced settings. Finally, rip-up clasts are seen within Bed 9 and these are also associated with high energy events like storms. This then would support the evidence put forward from the section at Ludford Corner by Smith and Ainsworth (1989).

Smith and Ainsworth (1989) suggested that the deposit at Ludford Lane represented a shoreface environment. Using this as a starting place, what evidence of a shoreface environment is there in the Weir Quarry section? The first line of evidence comes from the sedimentary structures seen with the section. Some of the planar laminations appear to have slight and subtle undulations; this suggests that they represent quasi-planar laminations (Text-fig. 3.21). These have been recognised as indicating single storm events (again supporting the storm dominated environment interpretation), but also being associated with a specific part of the shoreface (Arnott 1993), the lower shoreface. The reason for these planar and quasi-planar laminations is that on the lower shoreface it is below fair-weather wave base. This means that even though wave action was acting on the shoreline, the Weir Quarry section was below the depth where wave action would affect the bottom, resulting in these planar and quasi-planar laminations (Prothero and Schwab 2004; Reading 2009). However, during storm events, the wave base is deeper than fair weather and leaves a characteristic erosional contact and 'dumped' deposition (Prothero and Schwab 2004; Reading 2009).

It has now been established that the DBB was laid down during storms on a lower shoreface of a regressive coast, but is there any further environmental evidence that can be gathered from the section at Weir Quarry? Often within the five key papers (Allen and Tarlo 1963; Allen 1974; Antia 1980; Bassett et al. 1982; Smith and Ainsworth 1989) it is suggested that the PSM is a shallow-water deposit. Smith and Ainsworth (1989), when looking at Ludford Corner, admitted that they were unable to determine water depth. In their modern analogue, they compared Ludford Corner to the shoreline of Lake Huron which is stated to have a depth of < 2 m. At Weir Quarry (with a new interpretation of a lower shoreface) it is at least possible to give a depth range of 5-15 m (the depth to fair wave base), although this is not as shallow as the suggested depth of Ludford Corner of <2 m. The other common suggestion is that the PSM was deposited in a restricted environment. Evidence for this comes from the fossils present in the deposit. However, they will not be considered in this section as this is concerned only with the sedimentology; they will be discussed in Chapters 4, 5, 6 and 7.

The first and most apparent evidence for a restricted environment from the sediments comes from the syneresis cracks seen within Bed 9 (Text-fig. 3.22). These indicate a

change in salinity (Burst 1965) often seen in brackish water, which indicates a restricted environment. Another line of evidence for a restricted environment comes from the laminations in horizons 1 and 3, and at times 4. They show alternating laminations of sand and silt in a cyclic pattern. This could be an example of cyclic sedimentation (allocycles or autocycles). Allocycles are sedimentary cycles resulting from processes outside of the depositional system that involve forced oscillations of the sedimentary system. These could be caused by sea-level fluctuation, climate oscillations and tectonic activity all of which were occurring during the late Silurian (McKerrow et al. 2000; Munnecke et al. 2010; McConnell et al. 2019). Allocycles are also known to be exposed over a vast area and not restricted to a single basin. Autocycles are, by comparison, sedimentary cycles that are formed by processes that take place only within the basin of deposition and that include free oscillations of the sedimentary system; the subsequent cyclic succession is only a function of the characteristics of the geometrical and sedimentary parameters of the depositional system such as the shelf dimension and shape (Flügel 2004). Unlike allocycles, autocycles have limited stratigraphic continuity being restricted to a single basin. It is unclear which type of cycle the laminations of the DBB section represent. It should also be noted that cyclic sedimentation is usually associated with carbonates. The alternating sand and silt are also reminiscent of a sedimentary feature called varves. Varves are commonly seen in lake deposits, primarily from deposits in relation to seasonal melting of glaciers. The result is that bands of clay are deposited in yearly cycles, and these can be used for dating (Schimmelmann et al. 2016). They will not form in normal marine settings as the salinity causes the clays to flocculate and become coarser grains but they are recognised from brackish environments (Saarnisto and Ojala 2009). Allen (1985) suggested that the 'Downton' (Přídolí) sedimentation was at a rate of 2.5×10^{-4} Ma^{-1} due to the observation that no Ludlow rock sequence is thicker than 2 km and the Ludlow had a duration of approximately 2 Ma.

The DBB was formed when large storms picked up material from the Downton Sea bed. Finally, it would be disingenuous to make a blanket statement regarding the depositional setting of the entire DBB. The conclusion put forward both here and Chapter 9 must be viewed as representing only the DBB at Weir Quarry. However, in Chapter 9, a model will be put forward to account for the variation seen in the rock

record and a generalised model for the depositional setting based on observations, ex-situ material, and published literature.

4. Vertebrate palaeontology

4.1 Introduction

This chapter focuses on the vertebrates of the DBB at Weir Quarry. The chapter will discuss previous work that is of relevance to this study, and comment on the preservation of the vertebrate material, and describe all of the vertebrates. The descriptions are in the style of the journal *Palaeontology*. Finally, there will be a discussion of the findings of this chapter.

4.1.1 Previous work

The Silurian vertebrates of the Welsh Borders have been studied since the publication of Murchison's seminal *Silurian System* in which a contribution from Agassiz (1839) first described material from the region which was recovered from 'curious' deposits referred to as fish beds (later bonebeds). In the *Silurian System* Murchison and Agassiz described six genera and seven species: *Sphagodus pristodontus*, *Pterygotus problematicus*, *Plectrodus mirabilis*, *Sclerodus pustuliferus*, *Thelodus parvidens*, *Onchus murchisoni* and *O. tenuistriatus* as well as possible coprolites. Of particular note is *Pterygotus problematicus*, which was regarded as a fish but later identified as a eurypterid and then considered to be a *nomen vanum* (Kjellesvig-Waering 1961). Murchison (1853) discussed the presence of Crustacea within a bonebed of the "Upper Ludlow" (most likely the LBB), showing that the research into the bonebeds of the Welsh borders began early in the history of the study of Silurian strata. Professor Frederick M'Coy with whom Murchison was discussing the fossils, did not regard all of the newly discovered fish of the upper Silurian as fish. M'Coy suggested that *S. pustuliferus* and *O. murchisoni* were misidentified arthropods, while he regarded *S. pristodontus* and *T. parvidens* as the skin or scales of shark-like fish. Later, eurypterid workers like Kjellesvig-Waering (1961) pointed out that the samples that Murchison had labelled as *S. pristodontus* were the swimming limbs of a eurypterid. Strickland and Hooker (1853) commented on the distribution, and organic remains found in the LBB and mentioned only two fish by name, *Thelodus parvidens* and *Onchus tenuistriatus*.

Egerton (1857) published on fish remains in the Ludlow district focusing on the relative position of the strata that contained the fish fossils, but it is unclear exactly which beds he was studying. He does, however, refer to a bonebed and, given its location near the paper mill on the banks of the Teme between Ludlow and Ludford, he is likely to have been referring to the TBB. Egerton (1857) described three new fish from near Ludlow: *Auchenaspis salteri*, *Cephalaspis salweyi* and *C. murchisoni*. He also described some fragmentary material that he assigned to *Plectrodus*.
Murchison (1859) described the fossils of the upper Silurian (chapter 10, p. 237). Of note is his reference to discovery of the fishes *Pteraspis banksii* and *P. truncatus* in the "grey Ludlow rock". These were both later reassigned to *Cyathaspis banksii* (Lankester 1873; Lankester and Traquair 1914). Murchison (1859) referred to *Cephalaspis* noting its occurrence in the shale at Ludlow railway station. He also noted the presence of coprolites, once again mentioning that they contain fragments of invertebrates (molluscs and crinoids). He also reaffirmed that the fish in the Silurian of the U.K. were the oldest known in the world at that time. Despite fish fossils being found in Silurian rocks in America, Bohemia and Estonia, none was as ancient as those from the U.K. Huxley (1858) discussed in detail the history of the fish *Cephalaspis* and *Pteraspis* and their form and structure, including diagrams of the bone histology of both genera. He also considered their zoological position, suggesting that they belong either to ganoids (a loose association of fish base on their scales) or teleosteans (citing morphological similarities with modern armoured catfish).
Harley (1861) discussed Pander's (1856) earlier discovery in Saaremaa, Estonia of what he referred to as conodonts, but Harley felt that they were closer to crustaceans and erected the name Astacoderma. Roberts and Randall (1863) described the LBB from Linley Brook, later found to be the DBB (Stamp 1924).
Woodward (1904) recorded many of the previously decribed genera from the Ludlow district. He also provided an illustration of *Lanarkia spinosa,* which was related to *Thelodus,* which had also been found in the upper Silurian of Lanarkshire. Lankester and Traquair (1914) produced monographs on the fishes of the Old Red Sandstone and described the Cephalaspidae known at that time in detail. Straw (1927) looked at fish from the upper Silurian of Ludlow. He noted the recent changes of the stratigraphy that removed the LBB from Upper Ludlow strata; he also described the taxa *Thelodus parvidens*, *Onchus tenuistriatus* and *Cyathaspis*.

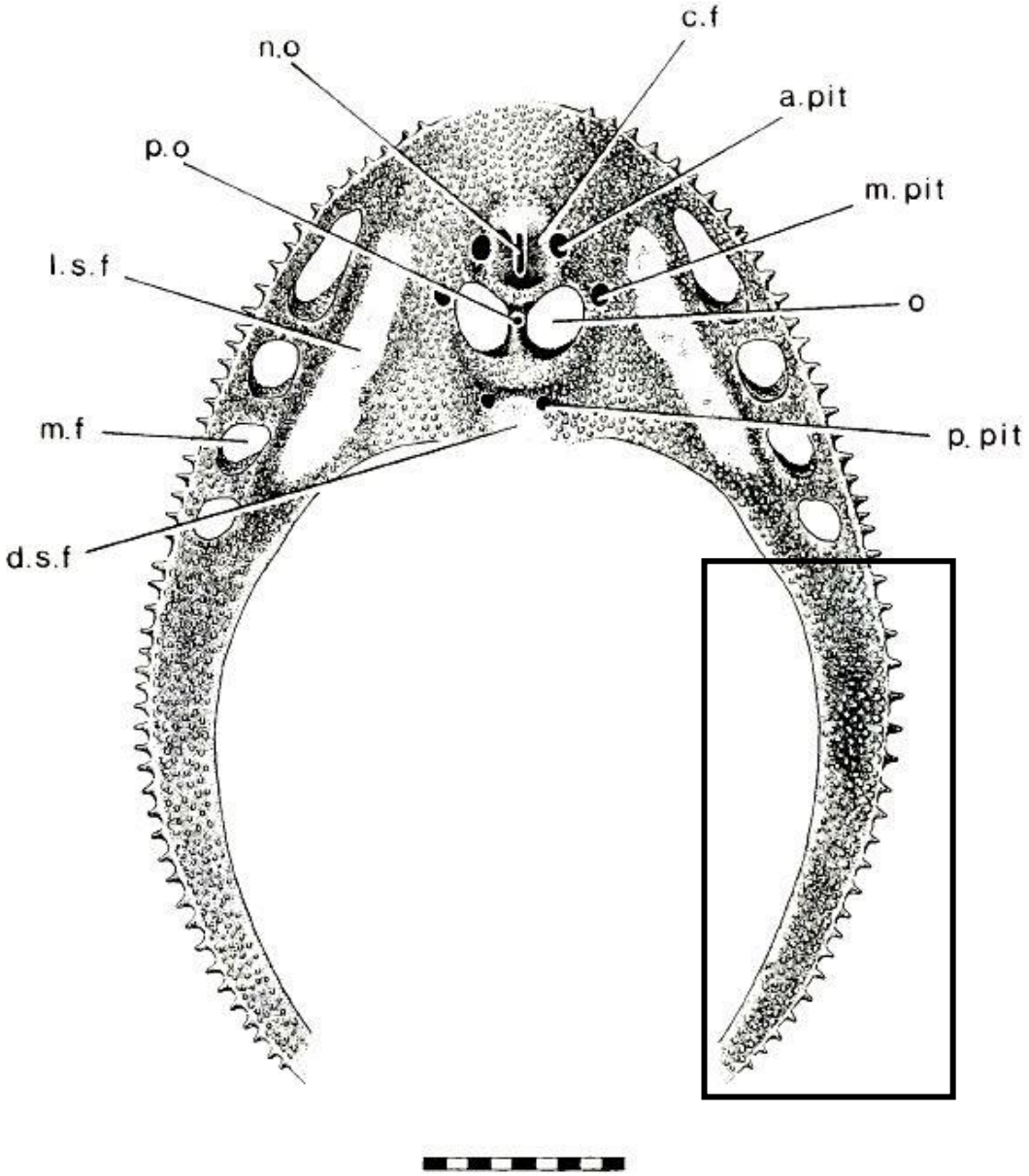
Straw (1933) described Silurian fossils found in a boring from Little Missenden in Buckinghamshire. The fossils, including some fish remains, were felt to represent the Downtonian (upper Silurian) in age. White (1935, 1945) described heterostracans from the Lower Old Red Sandstone Group higher in the geological sequence of the Welsh borders. Later, White (1950) described the vertebrate faunas of the Lower Old Red Sandstone from the 'Passage Beds'. White (1950) also put forward the concept of the LBB being the boundary between the Silurian and the Old Red Sandstone. By the late 1950s, a shift had been made back to investigating the LBB although at this point it was still regarded as latest Silurian and often was included within the Old Red Sandstone. Squirrel (1958) recorded new occurrences of fish remains from the Welsh borderlands, including from the LBB. Squirrel (1958) mentioned new thelodont and acanthodian occurrences but did not identify the taxa present. Allen and Tarlo (1963) mostly dealt with the sedimentology of the Downtonian and Dittonian facies of the Welsh Borderlands. However, they did comment on the facies and the vertebrates found within those facies. For the bonebed facies, they listed only *Sclerodus* and *Cyathaspis*.

Turner (1973) provided the first significant review of the vertebrates since the Welsh Borders were first studied, listing the thelodonts from each stratigraphical horizon, reviewing their systematics, and noting correlations with other localities locally and globally. At this time, most work on thelodonts had been carried out overseas (e.g. Gross 1967, 1968, 1971). The focus within the Welsh borderlands up to this point had been the osteostracans and heterostracans. This lack of interest in thelodonts is understandable, as thelodonts in the Welsh Borderlands were known only from disarticulated denticles making their affinities hard to ascertain. Earlier workers had, however, correctly identified the denticles as the squamation covering the body of the fish. Later workers who had the benefit of articulated specimens from Scotland (Märss and Ritche 1998) and the Baltic (Märss 1986) could then go back to the disarticulated remains, as Turner did and review the assemblages.

Aldridge (1975) described the stratigraphical distribution of conodonts the UK. He established conodont biozones, with the 'Downtonian' conodont faunas falling within the *eosteinhornensis* Biozone. This biozone included *Ozarkodina steinhornensis eosteinhornensis, O. confluens, O. excavata, Pelekysgnathus dubius* and *Distomodus dubius*. Subsequent workers have updated that work and the biozone that now includes the LBB and the DBB is the *Ozarkodina hemensis* Biozone (Märss

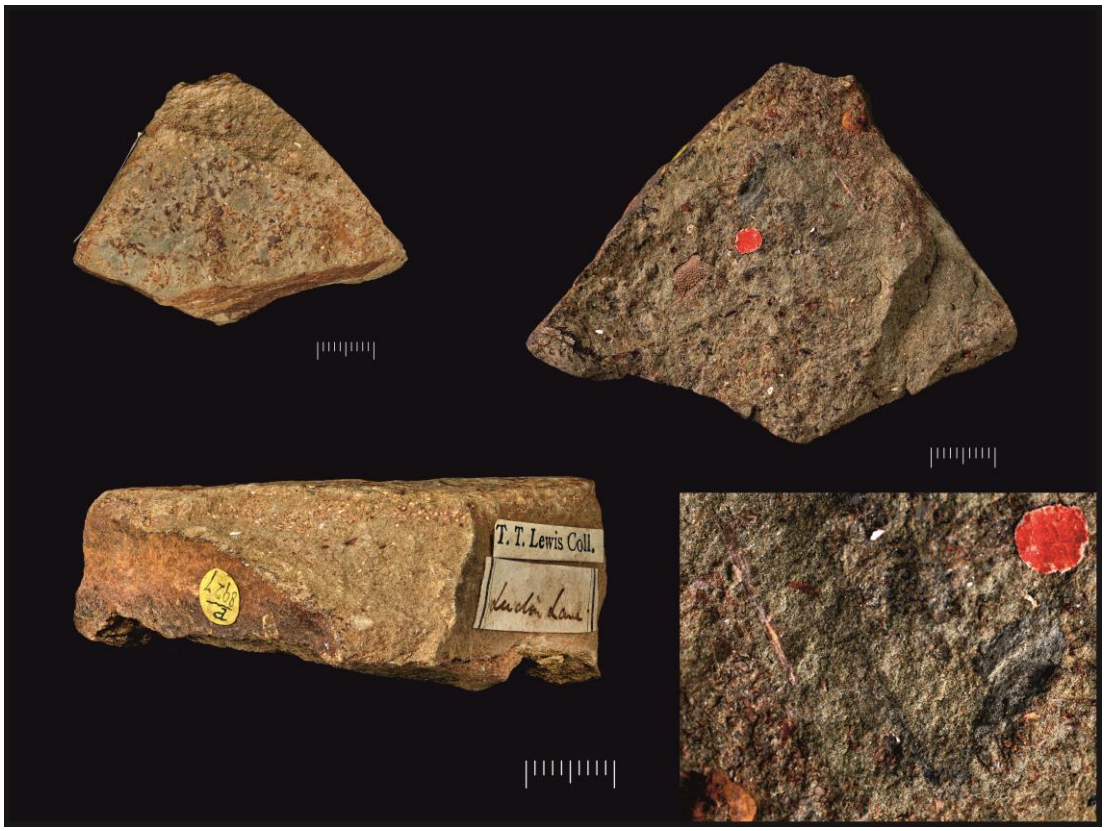
and Männik 2013). Halstead and Turner (1973) described the palaeobiogeography of the ostracoderms, including faunas from the Welsh Borderlands.

One of the most unusual ostracoderms from the DCSF is *Sclerodus pustuliferus*, which had a well-developed head shield. Forey (1987) reviewed the taxon, its morphology, physiology, and relationship to other Osteostraci. He suggested it to be a member of the Trematapididae. *Sclerodus pustuliferus* is recorded only from the "Downtonian" rocks of the Anglo-Welsh basin. Its rarity is reflective of this fish being interpreted to have been adapted to marine conditions and with the onset of brackish conditions (Allen and Tarlo 1963; Allen 1974; Cherns 2006) it became increasingly scarce. One of the specimens Forey studied was a part of the 'cornua', a part of the head shield that formed long spine-like projections toward the posterior of the fish (Text-fig. 4.1). This specimen is referred to as BMNH P.45315 collected by Whitaker and is figured in Chapter 3 of this thesis (Text-fig. 3.17). Forey (1987) included an appendix that listed sites from where specimens were collected but curiously it does not include BMNH P.45315, despite it being mentioned within the text. The appendix, however, does refer to a specimen (BMNH P.8927) from the Downton Castle Bone Bed, Lucton, Hereford and Worcester (Text-fig 4.2). This Downton Castle Bone Bed is presumably actually the DBB and serves as another example of how the DBB has been largely ignored and in some cases incorrectly named.



Text figure 4.1 Cephalothoracic shield of *Sclerodus pustuliferus*; box shows area described as the 'cornua'. The scale represents 9 mm (taken from Forey 1987, fig. 2 on p. 6) d.s.f dorsal sensory field, m.f marginal fenestra, l.s.f lateral sensory field, p.o pineal opening, n.o nasohypophysial opening, c.f circumnasal fossa, a.pit anterior pit, m.pit middle pit, o orbit, p.pit posterior pit.

The 1990s as a whole appear to have been quiet in regard to direct study of the vertebrates of the DCSF. However, Blondel (1992) and Vergoossen (1995) carried out research at this time. Vergoossen (1995) reported on acanthodian remains from Manbrook, Worcestershire, including the taxa *Nostolepis striata, Gomphonchus hoppei, Poracanthodes porosus, P. punctatus, P. stonehousensis* and Acanthodii sp. This fauna from the Upper Red Downton Group was compared to the Baltic fauna. It



Text Figure 4.2 BMNH P.8927 from the Downton Castle Bone Bed (most likely the DBB), Lucton, Hereford and Worcester. Scale bar represents 3cm.

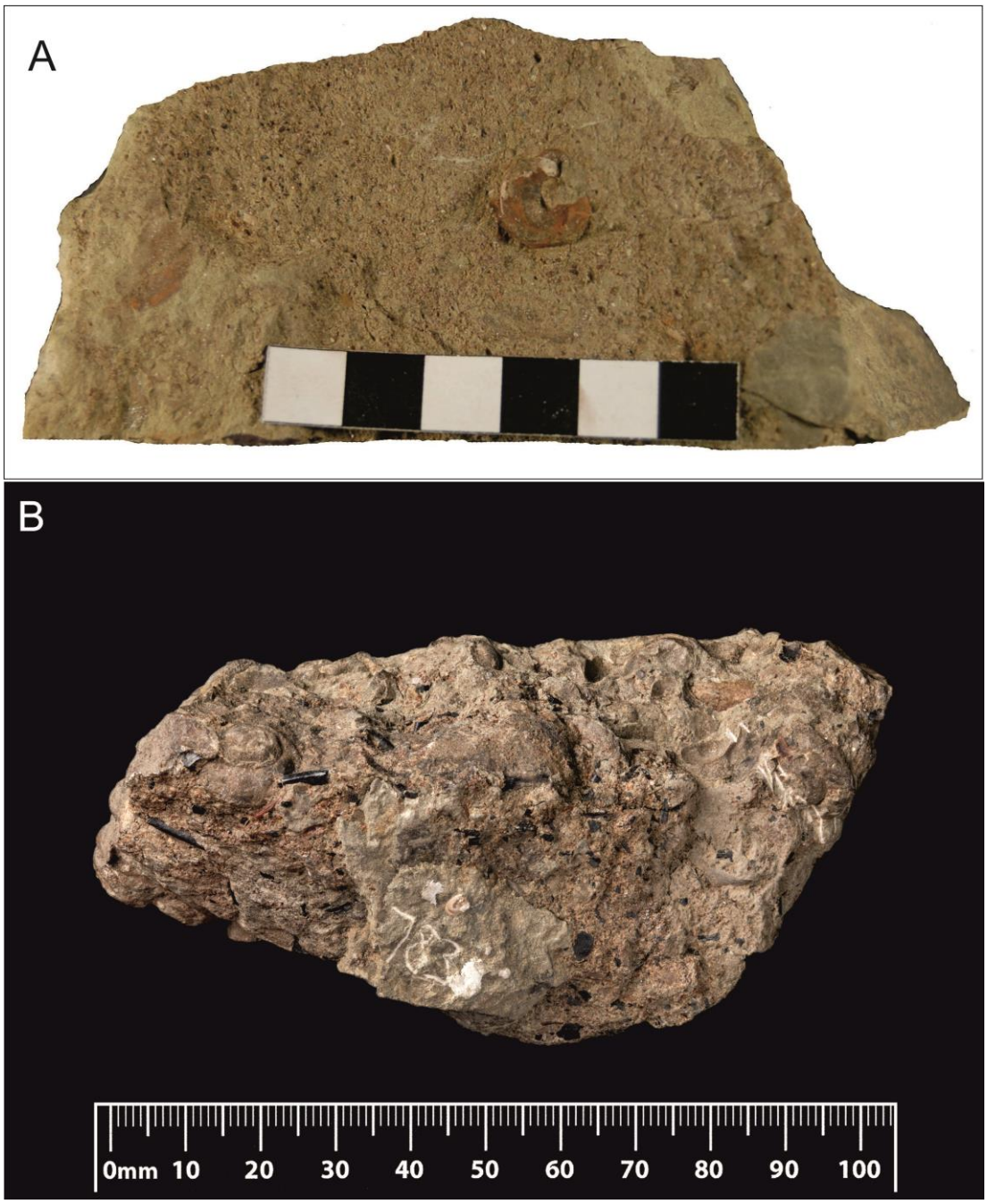
was considered that the differences in the fauna were the result of variation in shallow marine environments. By the end of the decade, a renewed interest in the bonebeds and the vertebrates of the Silurian of the Welsh borderlands had arisen. Miller and Märss (1999) described material from the historic Linley Brook, Shropshire locality. Their sample was collected from above the DBB within the Sandstone Member. Unlike most vertebrate fossils from the Welsh Borders, which are often in a poor state of preservation, often assumed to have been reworked from other deposits, Linley Brook material had superb preservation. The Linley Brook material was not recovered from a bonebed and appeared to have been deposited rapidly. The examples of *Paralogania ludlowiensis* have many of their spines of the scales in place, and Miller and Märss (1999) suggested that with these data it was possible to produce more accurate taxonomy, correlation and palaeoenvironmental reconstructions than before. The preservation of the conodonts was also good and of most importance is that they were present, as they are generally rare and reworked in the bonebeds of the Welsh borders, making them unsuitable for biostratigraphy. They also recorded a new species of acanthodian, *Nostolepis linleyensis*, noting that the

deposit represented marine conditions; this could be why they were in such a good state of preservation as it might represent deeper water than the DBB. In the same year, Dineley and Metcalf (1999) produced a Geological Conservation Review volume, which provided a comprehensive guide to the fossil fish sites known in the U.K. from across the Phanerozoic. Some of the sites were grouped into a combined chapter; this is the case with the DBB, which is included within the chapter '*Downtown Castle area: Downtown Castle Bridge, Tin Mill Race, Forge Rough Weir* (another name for Weir Quarry), *and Castle Bridge Mill, Herefordshire'*.
The volume provided an overview of the historical study, geology, gave fauna lists, and environmental interpretations; however, because it was concerned with many localities, the DBB did not receive the same attention as the LBB has had (Dineley and Metcalf 1999).
Turner (2000) and Vergoossen (1999a, 2000) reviewed acanthodian and chondrichthyan micro-remains from the Welsh borderlands. This provided a guide to acanthodian taxa that could be found within the DBB, including high-quality images of the taxa useful for identification purposes. Märss and Miller (2004) discussed thelodonts and the distribution of conodonts from the Llandovery-lowermost Lochkovian in the Welsh borders. They referred to the DBB once, and state "Downton Bone Bed thelodonts (sample 14c L. Jeppsson Lund University) did not differ from the Ludlow Bone Bed assemblage."

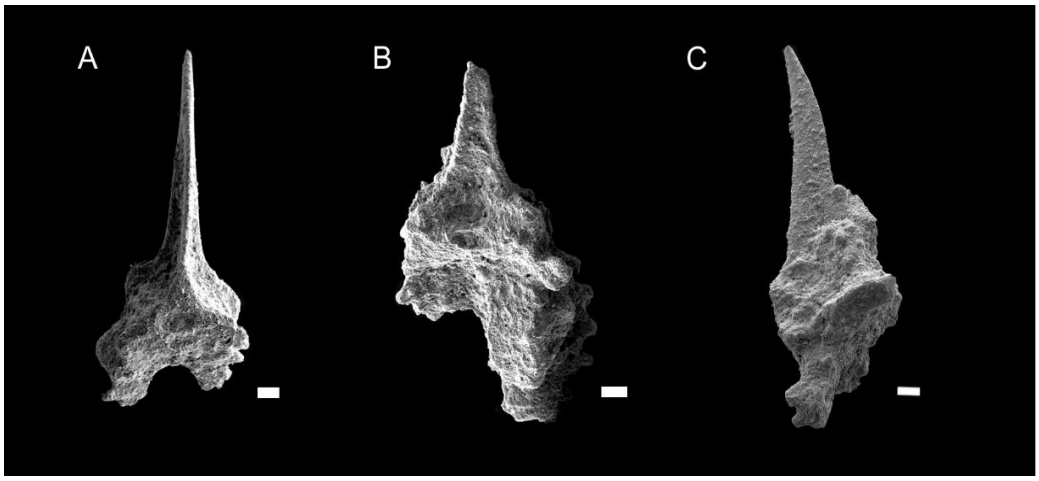
4.2 Preservation and Taphonomy

4.2.1 Preservation

The DBB appears to have two modes of preservation. At Ludford Corner and Weir Quarry, the vertebrate material has a polished orangey-yellow appearance. The thelodont denticles are missing spines. At Downton Castle Bridge and to the North, in addition to this first style of preservation some of the vertebrate material is highly polished and is black (Text-fig. 4.3). This study will focus on the material from Weir Quarry. Antia (1979) described two states of geochemical preservation. In the first the denticles are preserved in fluorapatite ($Ca_5 (PO_4)_3F$) and have a polished orangey-yellow appearance. The denticles of thelodonts were made up of dentine and dentine-like tissues and aspidine (acellular bone) (Vorob'eva 2012). Most acanthodian spines and denticles of acanthodians have bone tissue with osteocyte lacunae preserved (Valiukevicius and Burrow 2005). These were strong phosphatic tissues, which is why they are preserved as fluorapatite, which is still the mineralogical component of modern fish teeth (Deang et al. 2018). The second preservational state that Antia (1979) referred to is where the thelodont denticles have a chalky appearance, which he says occurs in the sediment below the LBB, and where they are preserved in carbonate apatite. This chalky appearance is seen in the three possible conodonts recovered from the DBB at Weir Quarry (Text-fig. 4.4). Anoxic microenvironments are found a few centimetres, below the sediment/water interface and these anoxic settings are suggested to be reason for this chalky appearance (Burnett 1977).



Text figure 4.3 Downton Bone Bed from A) Weir Quarry, and B) North of Downton Castle Bridge. Note the lack of polished black material in A. Scale represents 5 cm in A.



Text figure 4.4 Indeterminate conodont elements recovered from the DBB at Weir Quarry, A) WQ1a-A B) WQ1a-B C) WQ1c-G; scale represents 100µm.

4.2.2 Taphonomy

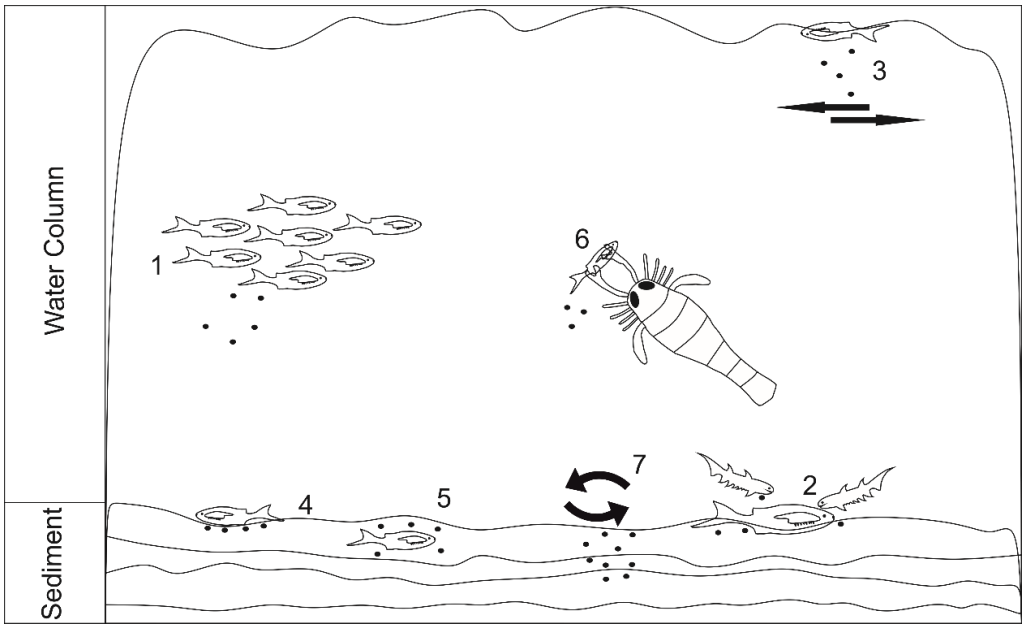
One of the essential considerations when establishing the taphonomy of an organism is to determine how the organism left the biosphere and entered the lithosphere. Although the DBB has various fish groups represented, it is the thelodonts that dominate in numbers, although not in overall diversity. Thelodonts will therefore be the focus of this section. As acanthodians were also cartilaginous fish with a micromeric squamation it is inferred that they would have been broadly susceptible to the same taphonomic processes.

Thelodonts are preserved in various states, from fully articulated specimens in Silurian strata of Scotland (Märss and Ritchie 1998) to the disarticulated, isolated material seen in the Welsh Borderlands (Turner 1973; Märss and Miller 2004). The taphonomy of Palaeozoic vertebrates has been discussed in detail recently (Burrow and Turner 2012). Although their focus was on Devonian fauna, they still discuss the formation of microfossil bonebeds. How organisms broke down through physical processes is assumed to have changed little throughout the Phanerozoic (Burrow and Turner 2012), while biological processes do appear to have changed (Kidwell and Behrensmeyer 1988). Only the dermal denticles of *Paralogania ludlowiensis* have made it into the rock record; this is not unexpected as thelodonts 'almost certainly' had a cartilaginous endoskeleton (Märss et al. 2007, pp. 13-22) which can break down quickly. Added to this, having a micromeric squamation suggests that they were more susceptible to taphonomic processes, unlike other armoured fish in the Palaeozoic, which had more firmly tied larger overlapping plates protecting the

carcass from disarticulation (Burrow and Turner 2012). The main destructive taphonomic processes and pathways by which the denticles could enter the lithosphere are described in detail by Burrow and Turner (2012). These include, disintegration and pre-burial decay, scavenging, transport and burial. However, two other factors affecting preservation should also be considered when discussing thelodonts: mode of life and predation. All of the processes and pathways are summarised in Text-fig. 4.5.

Disintegration and pre-burial decay are processes that are highly susceptible to variations in the environment; it has been stated that no studies have been carried out on the rates of disintegration on fish in the Devonian (Burrow and Turner 2012), this is presumably because there are no modern analogues. This also appears to be the case with the Silurian. Many studies have been carried out, however, on the disintegration and pre-burial decay of modern fish (e.g. Schäfer 1972; Weigelt 1989). It has been shown that the major factor that controls the breakdown of a carcass in the aquatic environment is temperature (Elder and Smith 1988), with lower temperatures slowing down the decay. With the interpretation of the climate during deposition of the Old Red Sandstone (including the DCSF) including a mean temperature of 16-20°C (Allen 1974), these warm temperatures probably meant that a carcass on the shallow seabed would probably decay relatively quickly. Another factor that impacts upon the rate of decay is salinity, with a higher salinity reducing the rate of bacterial decay (Burrow and Turner 2012). In subaerial conditions fish carcasses are exposed to other factors that can have an impact on the rates of disintegration and pre-burial decay, such as sunlight, rain, and wind; these are best demonstrated by Burrow and Turner (2012) (Text-fig. 4.6)

As a rule, larger individuals and larger animals with generally more substantial bones or plates are less susceptible to disintegration (Smith et al. 1988) than fish such as thelodonts with their micromeric squamation (Märss et al. 2003).



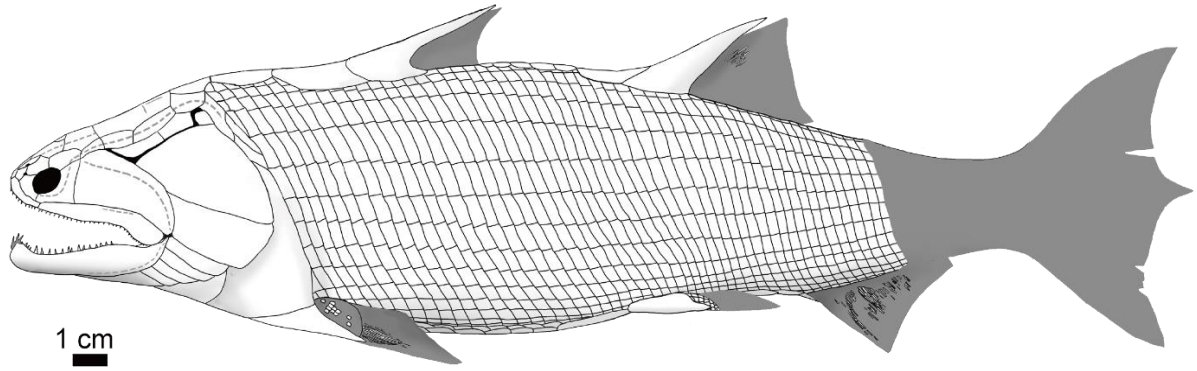
Text figure 4.5 Summary of all taphonomic processes and methods by which thelodont denticles could enter the lithosphere. 1) In life 2) scavenging 3) transport 4) disintegration and pre-burial decay 5) burial 6) predation 7) reworking; small circles represent denticles.

Text figure 4.6 Stages in the disintegration of four stranded freshwater drumfish (*Aplodinotus grunniens*), on the shore of Lake Manitoba, Canada, during the summer of 2003. (**a**) Soft tissues scavenged/ disintegrated and washed away; all dermal hard tissues remain in situ; (**b**) scattering of some fin rays, most of the squamation lost/removed on exposed side; (**c**) carcass at a similar stage of disintegration as b, but partially buried; (**d**) carcass after most exposed hard tissues have been scattered/scavenged (Photographs courtesy of Dr G. Hanke, Royal British Columbia Museum, from Burrow and Turner 2012).

Scavenging can interfere with the process of disintegration (Behrensmeyer and Hill 1980) whereas a carcass that is left undisturbed to disintegration processes will become disarticulated, it will still be in loose association (Barton and Wilson 2005). Scavenging disrupts this pattern; for example, the early post-mortem detachment of the lower jaw can be expedited by the presence of scavengers entering the mouth. They are assumed to access the soft tissue lining of the buccal cavity resulting in the detachment of the jaws. How susceptible thelodonts were to scavengers and what those scavengers were is a matter for further study. Indeed, by having an endoskeleton of cartilage (Märss et al. 2007) they would have quickly decayed unless buried in the right conditions. Which organisms were scavenging during the late Silurian is debatable. There are, however, contenders for this role. The first and most obvious are the largest marine organisms alive during the mid-Ludfordian, the eurypterids. There is also evidence from the Silurian of Scotland of eurypterids having fed on agnathans (Selden 1984). However, acanthodians are also present within the DBB, and being gnathostomes they could bite to catch prey, but also it could be inferred that they could have used this bite to scavenge other dead organisms. There is also *Onchus murchisoni* which although often considered an acanthodian has also been suggested perhaps to be a chondrichthyan; further study is required to determine where its affinities lie (Newman et al. 2017). Regardless, it has been suggested that some Late Devonian sharks *Ageleodus* and *Cynopodius* (Garvey and Turner 2006) may have had teeth adapted to scavenging, and it may also be that late Silurian chondrichthyans were also capable of scavenging, although no specimens have been found to support this inference.

Within the Ludfordian of Baltic and China, there is evidence of the first osteichthyans, *Andreolepis hedei*, an actinopterygian (Märss 2001), and *Guiyu oneiros*, a sarcopterygian (Zhu et al. 2009). While *A. hedei* is known only from scales, *G. oneiros* is a near-complete specimen (Text-fig. 4.7) with a well-developed jaw, and at 1 m in length, it seems reasonable to infer that it could have scavenged.

There is evidence within the lower LBB of sponge, microbial and fungal attack on the denticles of *Thelodus parvidens*, seen as minute borings (Antia 1979). However, these microborings have not been reported from any other deposit and have not been recorded from the DBB at Weir Quarry.



Text figure 4.7 Reconstruction of *Guiyu oneiros*, modified from Zhu et al. 2009.

Transport by water is often a key process in taphonomy; it is often responsible for dispersing a carcass over a wide area (Schäfer 1972). In fish, there is added complexity; not only will a carcass sat on the seabed be disturbed and disarticulated but if at the right water, depth wave and current action will move the elements over a far wider area (Burrow and Turner 2012). However, there is evidence that some Palaeozoic fish, at least, may have had the ability to bloat and float (Rogers and Kidwell 2007). This refers to the ability of a carcass to build up gases internally while decomposing, and has been recorded in other taxonomic groups (Schwimmer 1997; Mallon et al. 2018), allowing the body to float on the surface. Thus a fish carcass could not only drift along the bottom but perhaps after some time would drift to the surface, then would be acted upon by waves, while currents could drift the carcass over a larger area spreading more material (Schäfer 1972). Currents are very likely to have affected the arrangement of skeletal material in the DBB. Often currents can result in the alignment of elongate elements, while the shape of elements can affect their transport in currents, with rounded elements rolling, while rhombic and angular scales (such as those seen in thelodonts) are more likely to stay imbricated than round grains (Burrow and Turner 2012). This transport bias can result in winnowing that can have a powerful effect on the formation of microfossil bonebeds (Burrow and Turner 2012).

Burial of a carcass rapidly after death can slow the disintegration of the body. This is most common with benthic invertebrates (Brett and Seilacher 1991), although this has been seen in Silurian vertebrates with the articulated *Phlebolepis elegans* specimens from the Himmiste Quarry, Saaremaa, Estonia (Märss et al. 2003) and well-known specimens from Lesmahagow, Scotland (Zigaite and Goujet 2012) and Artic Canada (Wilson and Caldwell 1998). Of course, not all rapidly buried

specimens show exquisite preservation; this is because burial events can occur after a carcass has been sat on the seafloor where disintegration processes may have already taken place (Burrow and Turner 2012). The burial of a carcass can impair disintegration in two main ways: 1) enhancing sulphate reduction and linked with this 2) inhibiting or preventing scavenging and bioturbation. Burrow and Turner (2012) state "In marine sediments, the rates of sulphate reduction correlate with rates of deposition, and deposition of degradable organic matter affects the sedimentation rate. At increased rates of sedimentation, less degradable organic matter is decomposed by aerobic respiration, leaving more organic matter available for sulphate reduction" (Allison 1991).

Predation is a similar process to scavenging; however, the act of the animal (thelodont) being caught by a predator may have resulted in denticles being shed into the water column. Furthermore, while the thelodont is being eaten, this could also have deposited partially macerated material onto the seafloor before other pathways then influenced its preservation. Although there is little definitive evidence for predation upon thelodonts, there is agnathan material found in the coprolites of eurypterids (Selden 1984). Although mentioned in the scavenging section this only demonstrates that eurypterids consumed agnathans not that they caught them. The evidence of agnathan denticles in coprolites, suggests that there is another sub-pathway with denticles in coprolites being spread over a wider area than if the fish had died and disintegrated on the seabed.

One pathway that has not been considered before is that the denticles entered the lithosphere while the thelodont was still living. It has been suggested that thelodonts may have been able to shed and regrow new dermal denticles (Märss et al. 2007). Although it is unclear at what rate they did this, it was observed that isolated material often contains a mix of large and small denticles from the same taxon indicating either that young and old individuals were present and over time would replace their squamation (Märss et al. 2007) or that simply young and old fish died. This means that the thelodont would not have had to expire to record its presence in an ecosystem. Recently it has been suggested that some thelodonts, based on their squamations, favoured reef environments (Ferrón and Botella 2017) using their armour to protect themselves while squeezing into small recesses. Others, which are interpreted from articulated specimens to be dorso-ventrally flattened forms, are suggested to have been able partially to bury themselves into sand/silt (Ferrón and

Botella 2017). While there is no evidence of reefs in the DBB at Weir Quarry or anywhere else in the Welsh Basin at this time, it is not unreasonable to surmise that as thelodonts in life were dynamic, swimming animals, the denticles may have become damaged while still attached to the thelodont. These damaged denticles could then enter the fossil record.

The last process to discuss here is reworking. This has been described as crucial to the formation of the late Silurian bonebeds of the Welsh Borderlands and in particular the LBB (Burrow and Turner 2012). This process involves material that has been deposited and buried previously in sediment and is then excavated and redeposited. This often happens during storms when higher energy regimes prevail. Bones and other vertebrate material can also be incorporated in ravinement beds during marine transgressions (Rogers and Kidwell 2007). One of the critical aspects of reworking is that not only can it produce time averaging within a bonebed (Rogers and Kidwell 2007), but interpretations on the ecology of a reworked bonebed should be made cautiously as they represent allochthonous assemblages. There then becomes the potential for a bonebed to form in the absence in the environment of any of the organisms that make up its constituents, and that although the other pathways may have led to the original deposition of the skeletal and denticle material, it is the reworking that formed the bonebed. With the actions of other processes being overprinted, due to the length of time that the reworked material has been exposed, bonebeds often show a mixture of taphonomic states (Swift and Martill 1999; Rogers and Kidwell 2007).

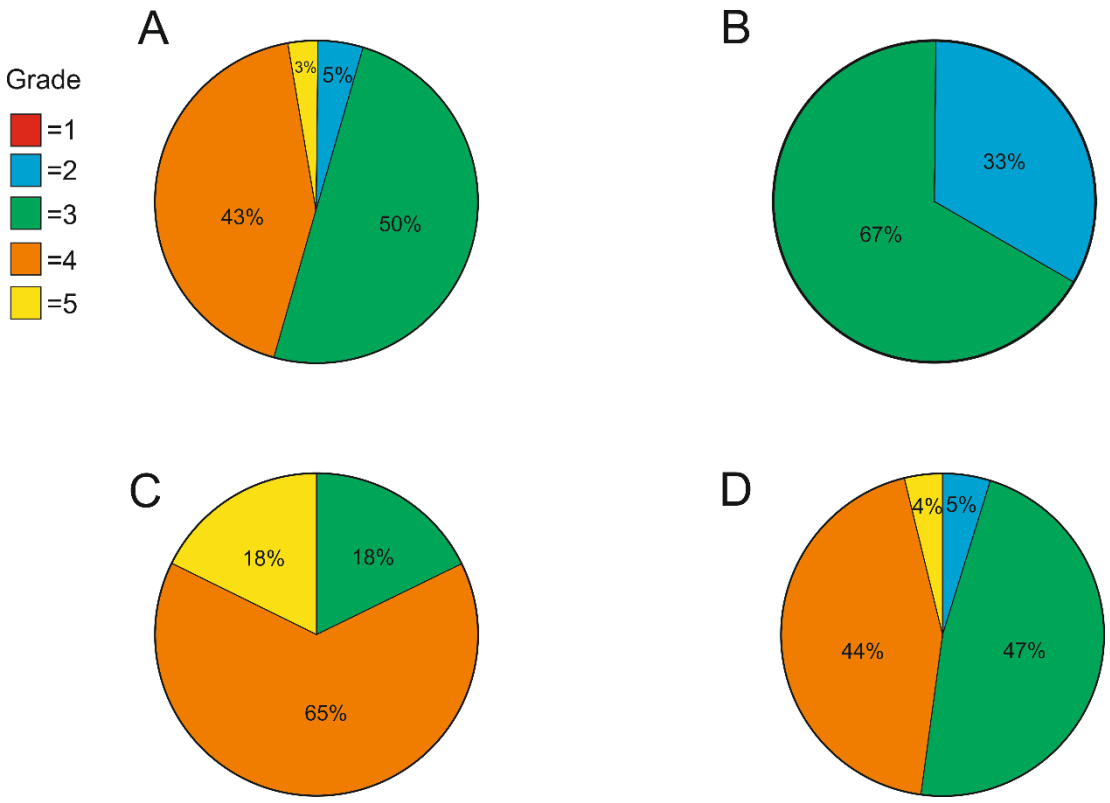
4.2.2.1 Taphonomic grade

To quantify the taphonomic data, a taphonomic grade was developed to indicate the amount of reworking, transport and damage that the fossils were exposed to before finally being deposited within the DBB, and to indicate whether the fossils accumulated over time or were rapidly buried. As thelodonts (*Paralogania ludlowiensis* trunk scales) are the most common and numerous fossil group in the DBB at Weir Quarry, they were chosen as the subject of the taphonomic grading (Table 2.1; Text-fig. 2.2).

Usually the entire range of taphonomic grades is used, comprising specimens from the deposit in question, i.e. in this case all of the fossils from the DBB; however, due

to the preservation of the denticles in the DBB, there is not a near-perfect specimen to use as the highest grade (i.e. best preserved). Therefore, a denticle recovered from Linley Brook by Miller and Märss (1999, pl. 2, fig. 18), was used as an example of a well-preserved (Grade 1) *Paralogania ludlowiensis* from the Welsh borderlands. The *Paralogania ludlowiensis* from Linley Brook were interpreted as having been buried rapidly (Miller and Märss 1999).

One limitation of this taphonomic study is that to produce the best results, quantitative data are required. However, the data collected for the most part were qualitative. This, of course, has an impact on the taphonomic grade data as the denticles were picked for their quality so that they could be identified to at least generic level. So, many denticles were not picked from the residues as they would not have been able to be placed with any accuracy in a genus. Despite the total number of identifiable and imaged *Paralogania ludlowiensis* denticles being 238, it does not reflect the abundance of the material in the DBB, and therefore an unintentional bias has been introduced. It is reflected in the results, as material-representing grade 5 is only 4% of the total amount of graded material (Text-fig. 2.2). Despite this, the data are still functional to assess the taphonomy. Although grade 5 is underrepresented, the second and third-lowest grade material is well represented (Text-fig. 4.8). The vast majority of the *Paralogania ludlowiensis* denticles in the DBB at Weir Quarry are lacking spines and many are not complete, missing portions of the base, neck and crown. The surfaces are also chipped and, as can be seen in 4 (Text-fig. 2.2), some surfaces show indications of abrasion.



Text Figure 4.8 Pie charts of taphonomic grade data of 238 *Paralogania ludlowiensis* scales from the DBB of Weir Quarry. A trunk scales, B head scales, C transitional scales and D all scale types.

The data show in Text-fig. 4.8 that overall no denticles were preserved to a grade 1 level, although a small number were found to be grade 2. The result supports the idea that the material that is found in the DBB at Weir Quarry was indeed subjected to transport and reworking before being deposited, as no denticles have been found with any processes left intact like those seen in Miller and Märss's (1999) Linley Brook sample. Instead, incomplete and abraded/broken specimens dominate, suggesting that they were exposed to higher energy levels during and probably before deposition; this would also account for the polished surfaces that the denticles show under light microscopy.

This suggestion of the denticles being exposed to higher energy regimes is supported in part by a study carried out by Brandt (1989) in which taphonomic grades were used to assess fossil assemblages and palaeoecology. A table was included that describes the relationship between timescale and energy within the environment (Text-fig. 4.9).

TIME SCALE	LOW ENERGY	HIGH ENERGY
Short-Term Deposition	little breakage, corrasion, high degree of articulation, no preferred orientation, high percent matrix, poorly sorted	high breakage, little corrasion, variable articulation, variable degree of orientation, variable amount of matrix, moderate- to well-sorted
Long-Term Accumulation	variable amounts of corrasion, high breakage, disarticulation, low degree of orientation, high percent matrix, poorly sorted	variable amounts of corrasion, high breakage, disarticulation, high degree of orientation, low percent matrix, well-sorted

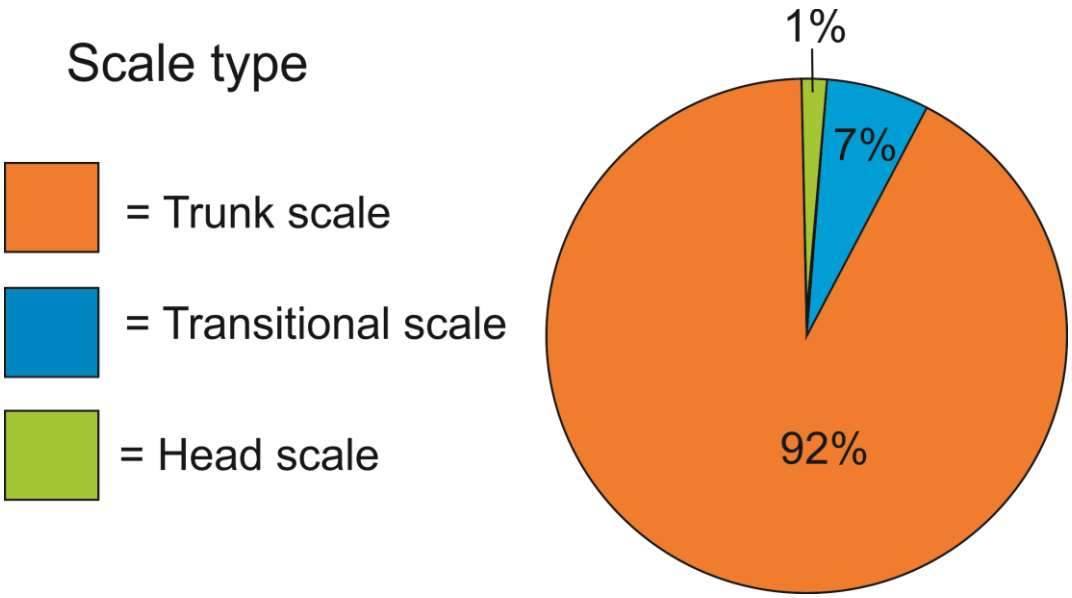
Text figure 4.9 Table 4 from Brandt (1989) illustrating the features seen between different time scales and energies.

The material from the DBB appears to fit with the description of Brandt (1989, table 4; Text-fig. 4.10) of long-term accumulation in a high-energy setting. This state is typified as being represented by "variable amounts of corrasion, high breakage, disarticulation, a high degree of orientation, low percent matrix, well-sorted". This is similar to what is seen in the DBB at Weir Quarry.

A significant factor in the formation of the Welsh Borders bonebeds is reworking (Anderton et al. 1979; Smith and Ainsworth 1989; Miller and Märss 1999; Cherns 2006). Evidence of this can be seen in the grade 5 material which is in such a poor preservational state that further reworking, abrasion and then burial would result in it being regarded as a phosphatic clast rather than a thelodont denticle. It seems likely that these denticles were exposed on the seabed potentially for years, being repeatedly exhumed and buried, before finally being deposited in the DBB at Weir Quarry. Grade 2 thelodonts appear to have been on the seabed for only a short duration before being deposited in the DBB. During that time, however, the spines present on many of the *P. ludlowiensis* may have been broken off from being transported and abraded on the seafloor. They equally could have been damaged by the event that deposited them into the DBB. Even in the grade 1 specimen some spines have already broken off, despite being buried rapidly in quiet waters as interpreted by Miller and Märss (1999). This suggests that only a small amount of energy would be required to cause breakage of the spines. It appears that a more important factor affecting the quality of preservation of the denticles is duration exposed on the seafloor to corrasion and transport. It is important to remember that the vertebrates of the DBB likely represent an allochthonous assemblage, and while high energy led to the deposition of the DBB at Weir Quarry, the denticles may not have been subjected to that level of energy for the entire duration that they were exposed on the seafloor. Being exposed for a more extended period on the seafloor may have allowed the denticles to be continuously transported, abraded and then

reworked into the DBB during a period of low background sedimentation (Anderton et al. 1979).

There appears also to be a bias as to which denticles are preserved. By far the most common type of *P. ludlowiensis* scale are the trunk scales (Text-fig. 4.10). The most logical reason is that of the estimated 20,000 dermal denticles covering the average-sized thelodont (Märss et al. 2007), one of the most common scale types will be trunk scales, as there is a greater surface area covered by these scales, as they are found across the body of the thelodont. Out of a total of 238 identifiable denticles from the DBB at Weir Quarry, 218 are identified as trunk scales. There are also 17 transitional scales. Finally, the rarest scale type in the DBB at Weir Quarry are head scales, with only three having been identified. This is most likely due to the head scales having the least surface coverage in relation to the other scale types as seen in the taxon *Phlebolepis elegans*, resulting in them being being poorly represented.



Text figure 4.10 Pie charts of taphonomic grade data (n=238).

4.3 Systematic Palaeontology

Phylum Chordata Haeckel, 1874

Subclass Thelodonti Stensiö, 1958

Order Shieliiformes Märss, Wilson and Thorsteinsson, 2002

Family Shieliidae Märss, Wilson and Thorsteinsson, 2002

Genus PARALOGANIA Karatajūte-Talimaa, 1997

Type species: *Paralogania ludlowiensis* Gross, 1967; from the Ludlow Bone Bed Ludlow, Shropshire, UK

Paralogania ludlowiensis Gross, 1967

Plate 4.1 Figures A-R, Plate 4.2 Figures A-R, Plate 4.3 Figures A-I, Text Figure 4.11 A

1967 *Logania ludlowiensis* Gross, p. 41, pl. 5, figs 43–48; text-fig. 13R–X.

1973 *Logania ludlowiensis* Gross; Turner, text-fig. 4c.

1978 *Logania ludlowiensis* Gross; Karatajūte-Talimaa, p. 95, pl. 25, figs 24–26; pl. 26, fig.13.

1978 *Logania ludlowiensis* Gross; Antia and Whitaker, figs 1c–e, j, 3d.

1986 *Loganella* sp. cf. *L. ludlowiensis* (Gross); Turner, pp. 9, 12.

1990 *Loganellia ludlowiensis* (Gross); Märss, pl. 19, fig. 8.

1991 *Loganellia ludlowiensis* (Gross); Turner, p. 105.

1997 *Paralogania ludlowiensis* (Gross); Karatajūte-Talimaa, p. 124, text-fig. 7f.

1999 *Paralogania ludlowiensis* (Gross); Miller and Märss, p. 700, pls 2-4.

2004 *Paralogania ludlowiensis* (Gross); Märss and Miller, p. 1232, pl. 2, figs 1-15.

Holotype: Gross, 1967, pl. 5, fig. 47, PMB f. 976, Institut für Paläontologie, Museum für Naturkunde, Humboldt Universität, Berlin; Ludlow Bone Bed, middle Ludfordian, Silurian; Ludlow, Shropshire, UK.

Material: 238 identifiable scales with most being from the trunk (92%), also transitional (7 %) and head (1 %) from material collected and recovered from the

DBB at Weir quarry, Herefordshire, U.K. 1 trunk scale in thin section (Text-fig. 4.11 A).

Diagnosis (after Märss, Turner and Karatajūte-Talimaa 2007): Large, narrow to broad, navicular scales; anterior edge of the crown rounded, curving out and back to the distal point; trunk scales with a raised, smooth rhombic crown, some varieties with a median groove or trough, sides of the crown almost vertical, curving into a horizontal neck groove, which can be wide anteriorly; narrow oblique ledge on each side of the posterolateral edge of the crown, which rises from the midpoint of the distal point; minor ledges can be present; typically five pairs of spikelets or knobs below the ledge, knobs point obliquely backward; the rows end as a pair of knobs under the distal point of the crown; circular to oval base with a deep concave pulp depression in young scales; pulp cavity reduced to a slit leading to the pulp opening in older scales; anterior base sometimes swelled, with an anterior spur; fine dentine canals sometimes swollen in their lower half, forming enlarged lacunae; the central dentine canals have the widest branching in mid-course. Anastomosis of dentine canals can be present; dentine canals passing from the short pulp canal into the lateral spines and giving rise to numerous fine dentine tubules in the upper distal crown, neck, and base. "Pronghorn" shaped scales are probably special scales of the cephalothorax: these small cuboid scales with a steeply upturned crown ending in a distal point, a high neck with one or two pairs of small prongs or knobs on the posterolateral surface, and, rarely, small riblets on the neck; oval base swollen anteriorly in older scales.

Description:

Trunk scales: (Plates 4.1-4.2) Large, broad to narrow oval to lenticular scales, rounded at the proximal end and tapering posteriorly to the distal end. Smooth rhomboidal crown. Neck curving gently to the base can show minor ledges. Below ledge typically between 5-9 bases of spines can be seen. These are all broken in examples from the DBB. The base is rounded at its margins and always wider than the crown, deep concave pulp in younger scales but reduced to a slit in older scales.

Head scales: (Plate 4.3 figs G-I) Small scales (length of base 0.21-0.31 mm) taller (0.3-0.5 mm) than other scales with one medial vertical, rounded cone directed

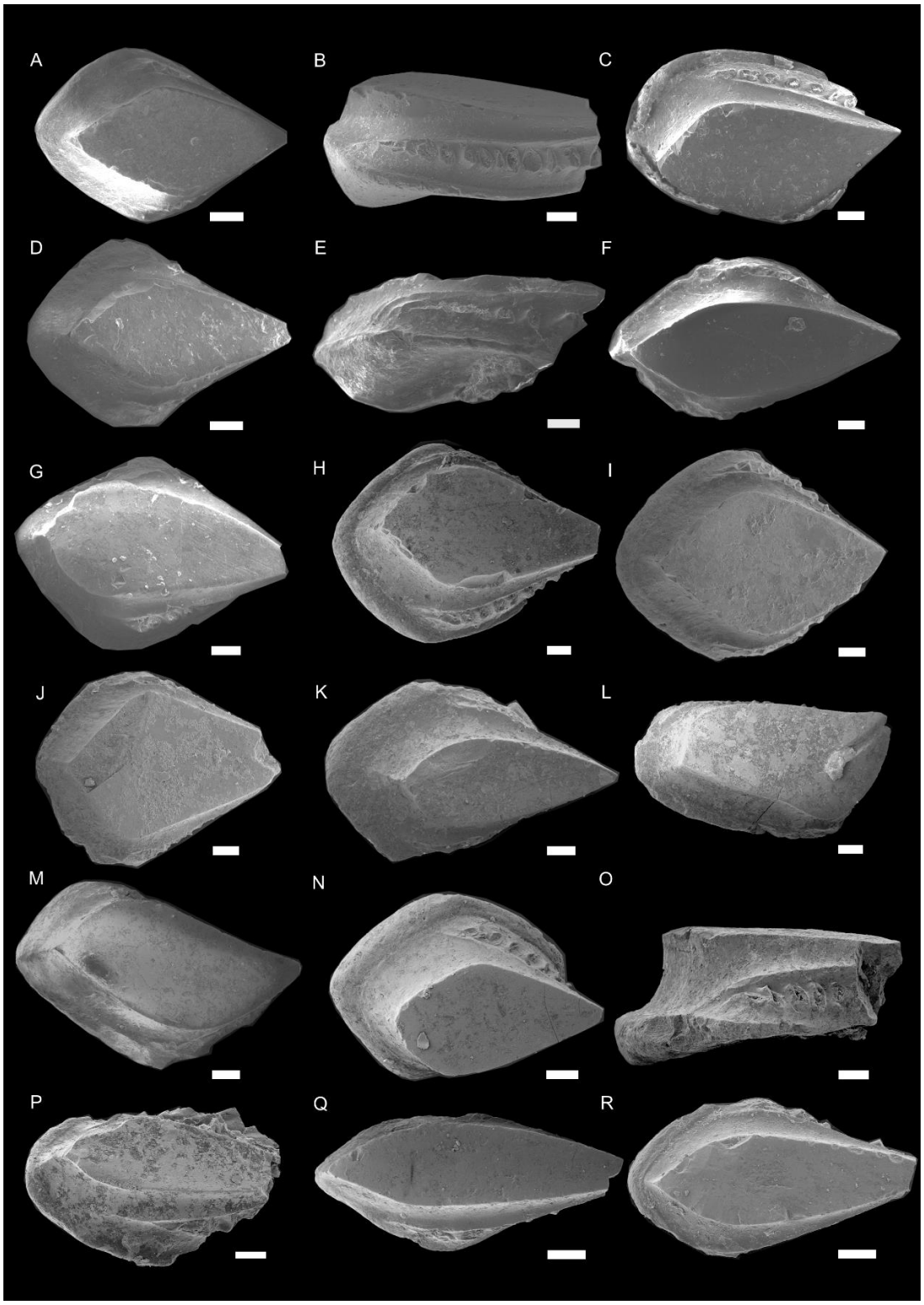
posteriorly and surrounded by the broken bases of hornlets; the hornlets are located anterior of the scale and are directed towards the main cone. Some of the hornlets are flattened, and more scale-like (Plate 4.3 fig. G); the hornlets are found in close pairs. The neck is high and lacks vertical ribs, base oval with rounded edges (Plate 4.3 fig. H); other examples appear to have less rounded edges to the base. The base is wider than the crown.

Transitional scales: (Plate 4.3 figs A-F) These scales are flat or have a narrow-raised crown; very different morphologies are most likely due to being transitions from different parts of the body, with a range of sizes (0.5-0.7 mm taken from complete examples). Spines can be found at the same level as the surface of the crown below the shallow ledge (Plate 4.3 fig. B). Crown points posteriorly with some smaller scales having two longitudinal ridges (Plate 4.3 fig. 5 A, C). On the base of scale, opening of pulp cavity visible although is small (200 µm).

Histology: Well developed pulp cavity in trunk scale beginning in the medial part of the scale and extending to the distal point of scale (Text-fig 4.11 A). Small brown, often bifurcating dentine tubules on the margin of denticle excluding proximal tip which is devoid of such structures. On the lateral exterior of the denticle, the broken bases can be seen.

Remarks: Material used for descriptions and histology is limited in the detail it provides due to its preservation quality; for further information see Miller and Märss (1999) which provides regionally and temporally similar material to the DBB. The transitional scales described here are tentatively assigned to *Paralogania*.

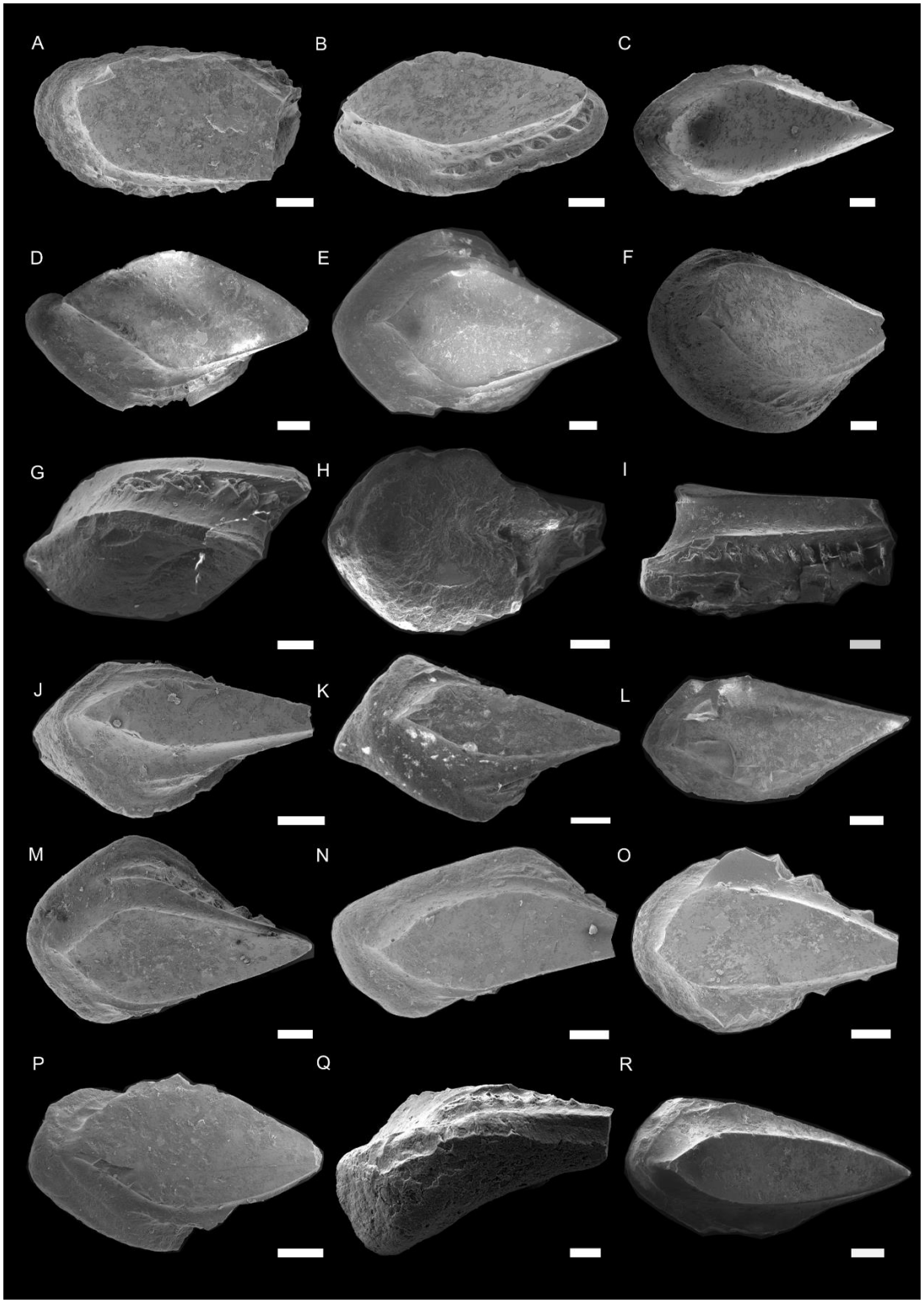
Plate 4.1



Explanation of Plate 4.1

Figs A-R *Paralogania ludlowiensis* (Gross, 1967): trunk scales, A) DBB5.500.1, B) DBB4.500.4, C) DBB4.500.3, D) DBB4.500.5, E) DBB6.500.1, F) DBB4.500.2, G) DBB20B.500.4, H) DBB20.500.1, I) DBB.500.f, J) DBB20.500.28, K) DBB5.500.8, L) DBB20.500.16, M) DBB20.500.22, N) DBB5.500.1a, O) DBB5.500.21, P) DBB20.212.1, Q) DBB20.500.2, R) DBB20.500.41. A, C-D, F-J, Q-R, in crown view. B, E, O, in lateral view; K, N, oblique lateral view of neck; L and P, oblique lateral view of the crown. Scale bars represent 100 µm, Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

Plate 4.2



Explanation of Plate 4.2

Figs A-R *Paralogania ludlowiensis* (Gross, 1967): trunk scales, A) DBB20.500.30, B) DBB20.212.7, C) DBB20.500.33, D) DBB.500. j, E) DBB.500.v, F) DBB.500.z, G) DBB20B.212.2, H) DBB7.212.7, I) DBB20B.212.3, J) DBB5.212.10, K) DBB.212.au, L) DBB.212.bj, M) DBB5.212.2, N) DBB5.212.1, O) DBB.212.19, P) DBB.212.13, Q) DBB.212.6, R) DBB18.212.2. A, C, E, L, N, O and R in crown view; I and Q in lateral view; B, D, F, J, K, M and P oblique lateral view of neck; G, oblique lateral view of the base; H in base view. Scale bars represent 100 µm; Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

Order Thelodontiformes Kiaer, 1932

Family Coelolepididae Pander, 1856

Genus THELODUS Agassiz, 1838

Type Species. Thelodus parvidens Agassiz, 1839, Ludlow, Shropshire, U.K.

Thelodus parvidens Agassiz, 1839

Plate 4.3 Figures J-N, Text Figure 4.11 B

1839 *Thelodus parvidens* Agassiz; Murchison, p. 647, figs 34, 36.
1856 *Thelodus parvidens* Agassiz; Pander, p. 64, Tab. 5.
1973 *Thelodus parvidens* Agassiz; Turner, p. 561, figs 3, 4.
2004 *Thelodus parvidens* Agassiz; Märss and Miller, p. 1248, text-fig. 12.

Holotype: Identified by Turner (1973, p. 562); GSM Geol. Soc. Coll. 6746, recorded by the British Geological Survey as probable type material.

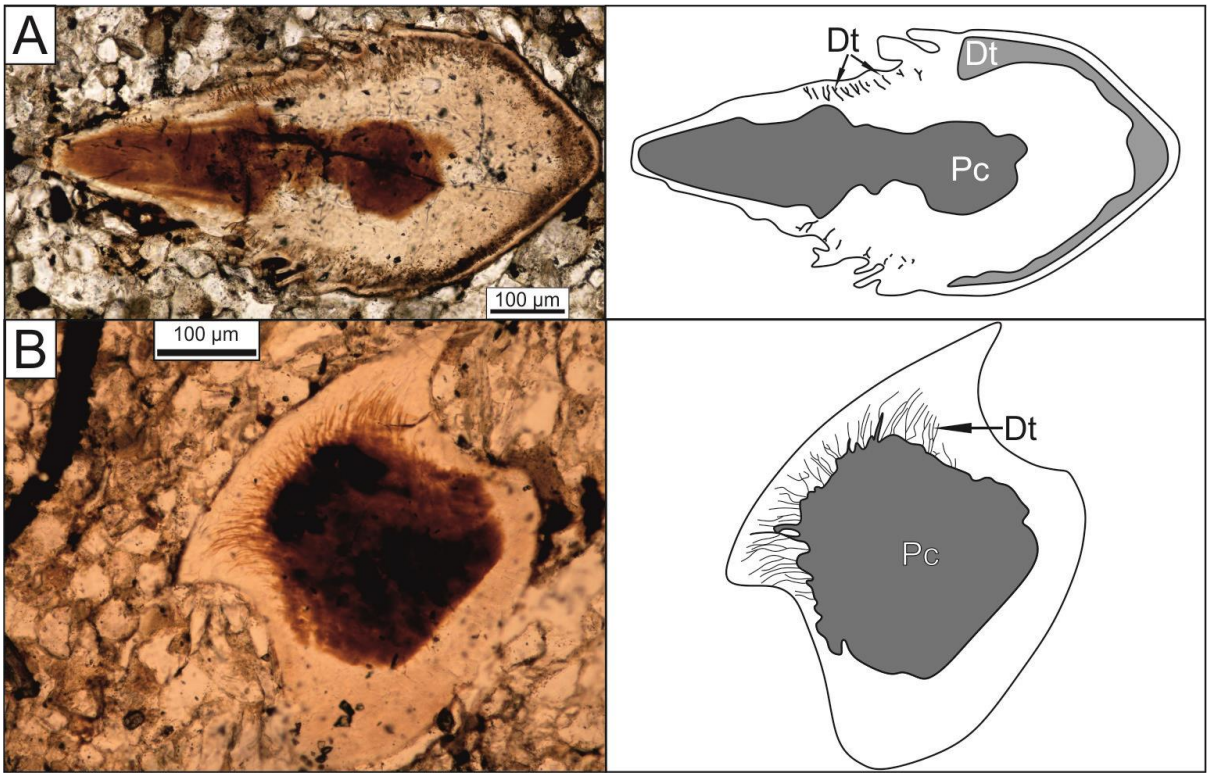
Material: 11 in total; nine trunk scales collected from the residues prepared from the DBB at Weir Quarry. Two trunk scales in thin section.

Diagnosis (after Märss, Turner and Karatajūte-Talimaa 2007): Rhombic to circular scales; anterior crown angular or rounded, posterior angle acute, surface of the crown smooth and planar, or with downturned anterior edges, rim of the crown plain; necks gently incurved with, typically, 3-12 small vertical riblets on the posterolateral, and, sometimes, on the anterolateral, surface. The species contains biostatoform, costatiform, trilobatiform, and traquairiform scales.

Description: Large flat crown lacking ornamentation, the neck tapers gradually towards the base, the neck has distinctive vertical ribs around the neck, the base is rounded, often with a pore present (Plate 4.3 figs J-N).

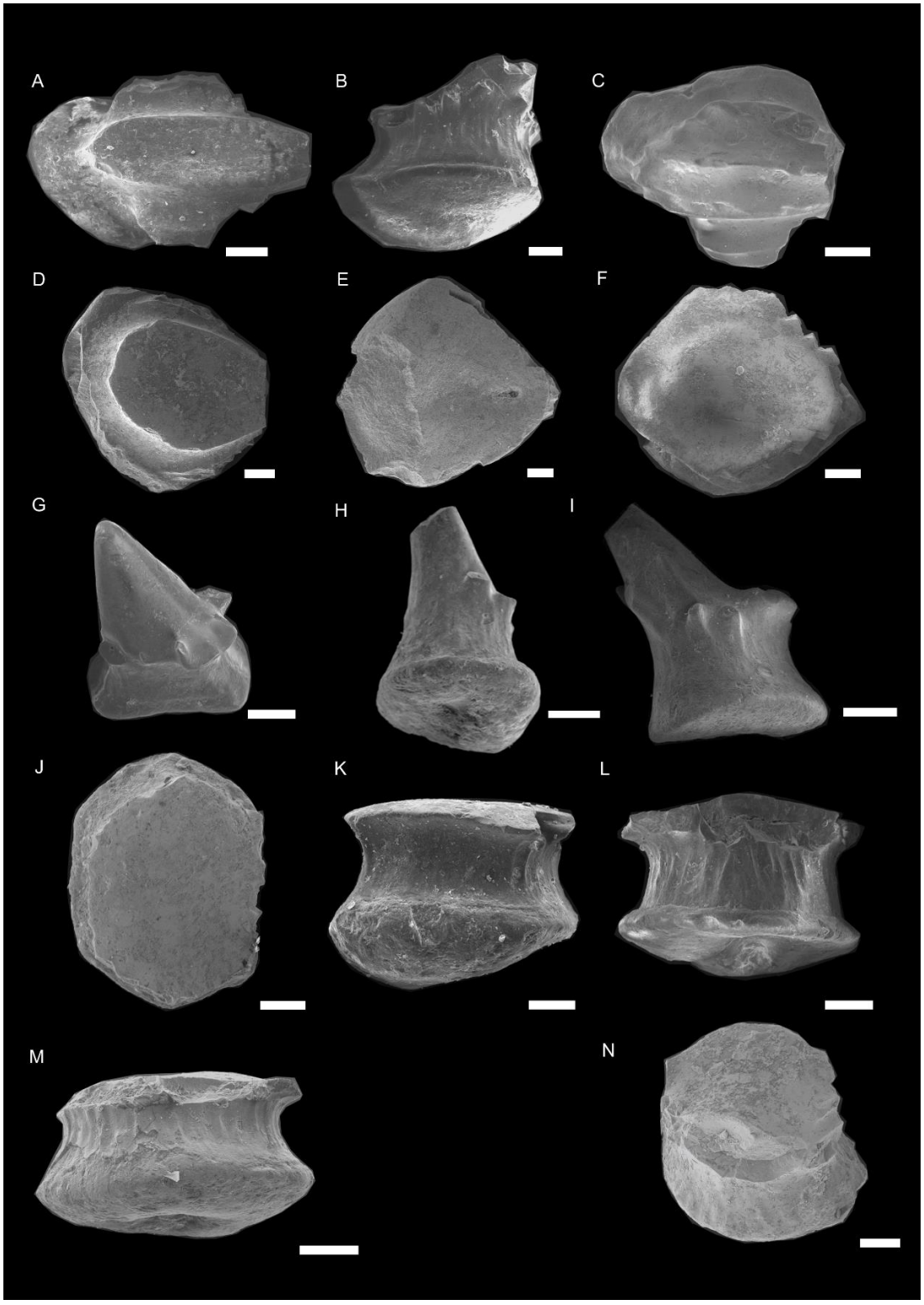
Histology: Large well-developed pulp cavity in the centre of denticle (Text-fig. 4.11 B). Finely branched dentine tubules radiating to the crown.

Remarks: Due to the poor preservation of *T. parvidens* specimens, it is challenging to give a more detailed description. For a more detailed description of this taxon from Ludford Corner, Ludlow, U.K., see Märss and Miller (2004, p. 1248).



Text figure 4.11 Histology of thelodonts in the DBB, A: *Paralogania ludlowiensis* in crown view. B: *Thelodus parvidens* in lateral view; line drawing has been rotated for convenience. Pc, pulp cavity; Dt, dentine tubules (light grey area represents a mass of Dt).

Plate 4.3



Explanation of Plate 4.3

Figs A-I *Paralogania ludlowiensis* (Gross, 1967): A) DBB4.212.1, B) DBB4.500.3, C) DBB.212.br, D) DBB5.500.3, E) DBB20.500.23, F) DBB19.500.3, G) DBB.212.j, H) DBB.212.r, I) DBB.500.U. A-F cf. *Paralogania ludlowiensis*. transitional scales; G-I head scales. J-N *Thelodus parvidens* (Agassiz, 1839), J) DBB.212.17, K) DBB.212.2, L) DBB.212.aq M) DBB5.212.4, N) DBB20.500.6, trunk scales. A, D, F, J in crown view; B in oblique lateral view of the base; C and N in oblique lateral view of neck; E in base view; G-I and K-M in lateral view. Scale bars represent 100 µm, Downton Bone Bed, Ludlow Series, Silurian, Weir Quarry, Herefordshire, UK.

GNATHOSTOMATA

Class Acanthodii Owen, 1846
Order Ischnacanthiformes Berg, 1940
Family Ischnacanthidae Woodward, 1891
Genus GOMPHONCHUS Gross, 1971

Type species. *Gomphonchus sandelensis* Pander, 1856, Saaremaa, Estonia

Gomphonchus sp.
Plate 4.4 Figures A-C, Text-Figure 4.12 A

Material: 2 scales, and two fragments of tooth whorl collected from the residues prepared from the DBB at Weir Quarry.

Diagnosis (after Denison 1979): A genus based originally on scales which are variously formed, with a low or convex base, and with a low or elevated crown that may be smooth or ornamented with radiating ribs. The base is cellular bone rarely penetrated by fine canals from the inner surface. The crown is dentine with thin layers of enameloid on top, without a well-developed canal system, but with long dentine tubules that rise in the neck and turn towards the centre of the crown top, giving off side branches. Lateral line scales include a pore-canal system consisting of radial canals entering at the neck, arcade canals, and pore canals opening on the surface of the crown. Stellate platelets from the head have apposed rather than superposed growth zones. The dentigerous jaw bones bear a single row of teeth that are typically circular in parabasal section (though jawbones bearing teeth with a triangular section and with a medial row of denticles, may belong here.) Tooth spirals carry teeth with a large cusp and small side cusps. Single teeth have a tall conical cusp and minute cusps around the base. Teeth consist of dentine. Fin spines are slender, nearly straight, and usually ornamented with smooth, longitudinal ribs of which the anterior rib is largest; the ribs may subdivide and may be slightly noded or crossed by furrows. Spines may have a small inserted base and are composed entirely of dentine except for a thin basal layer of bone.

Description:

Trunk scales: Large "kite"-shaped crown, which tapers posteriorly (Plate 4.4, fig. A); anterior of crown possesses crenulation with three distinct "lobes" in the central edge; neck shallow with a projection on the lateral edge where it joins with the base. The base is deeply convex (Plate 4.4, figs A, B); this is missing on the second specimen due to poor preservation.

Tooth whorl: Both fragments are badly broken; both show ankylosed teeth, which are broken.

Remarks: There are also two fragments of tooth whorl, which are identified as cf. *Gomphonchus* sp. As *Gomphonchus* belongs to the Ischnacanthiformes, an order known for having robust dermal gnathal bones this would be the most logical taxon to assign the fragments of tooth whorl (Plate 4.4, figs O-N).

Order Climatiiformes Berg, 1940

Genus NOSTOLEPIS Pander, 1856

Type species. *Nostolepis striata* Pander, 1856; Ohesaare Cliff, Saaremaa, Estonia

Nostolepis sp.

Plate 4.4 Figures D-E

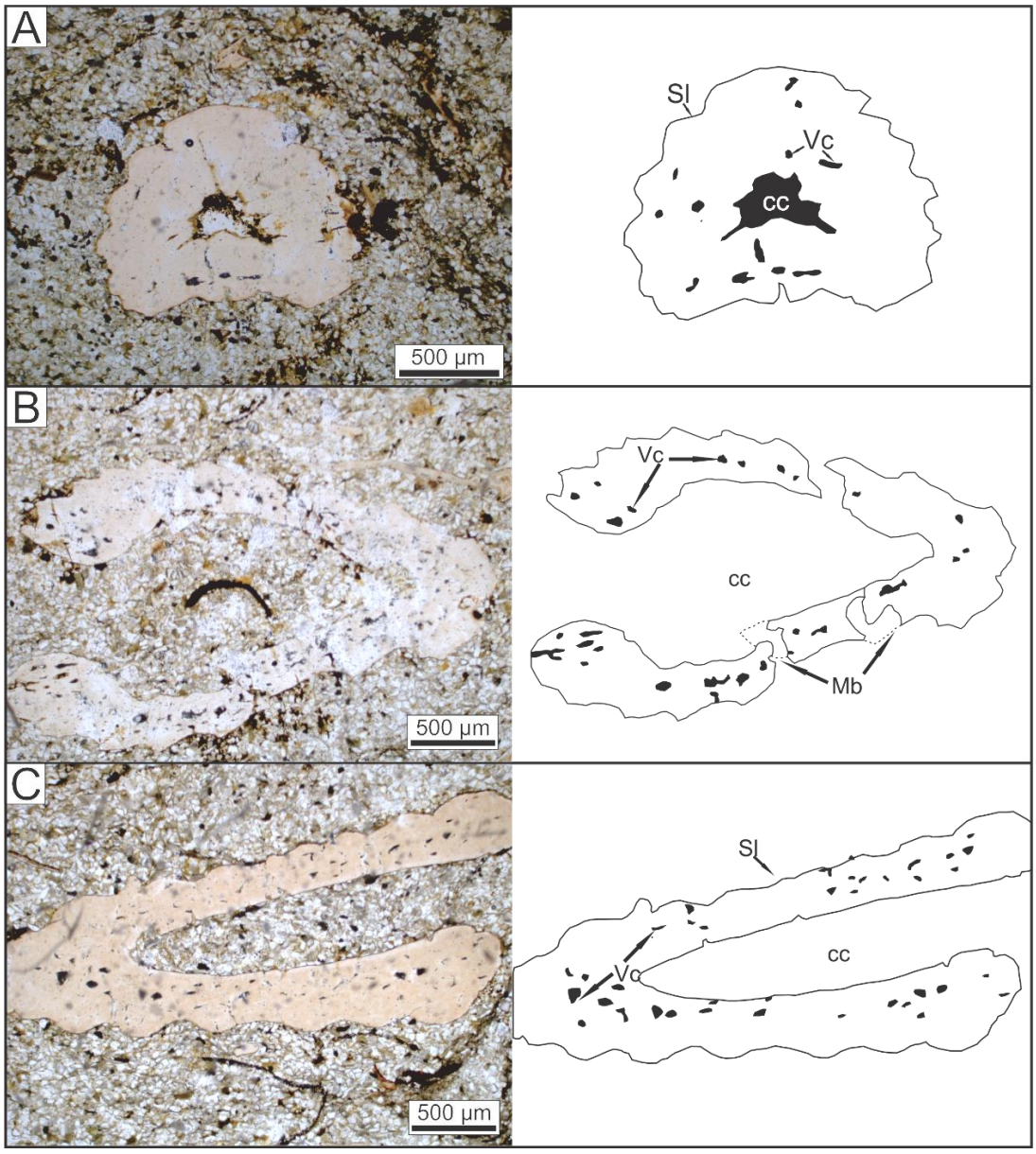
Material: 2 partial platelets, collected from the residues prepared from the DBB at Weir Quarry.

Diagnosis (after Denison 1979): A genus originally based on scales, which are variously ornamented with converging or parallel ridges, or with strong ribs. Scales are characterised particularly by their histology: the crown is formed of mesodentine and Stranggewebe, and is penetrated by a system of radial, concentric and ascending vascular canals from which mesodentine tubules arise; the bony base has numerous lacunae. The head is covered by a variety of tesserae which are ornamented with clusters of tubercles and have similar histology to scales. Tooth spirals bear transverse, leaf-shaped teeth composed of mesodentine peripherally and to trabecular dentine centrally in fully developed teeth; the bony base is cellular. Fin spines are

ornamented with nodose ridges and lack an inserted base; their ridges are composed of mesodentine, the middle and basal layers consist of cellular bone, and the central cavity is filled in mature spines with an osteon of cellular bone. Paired intermediate spines are present.

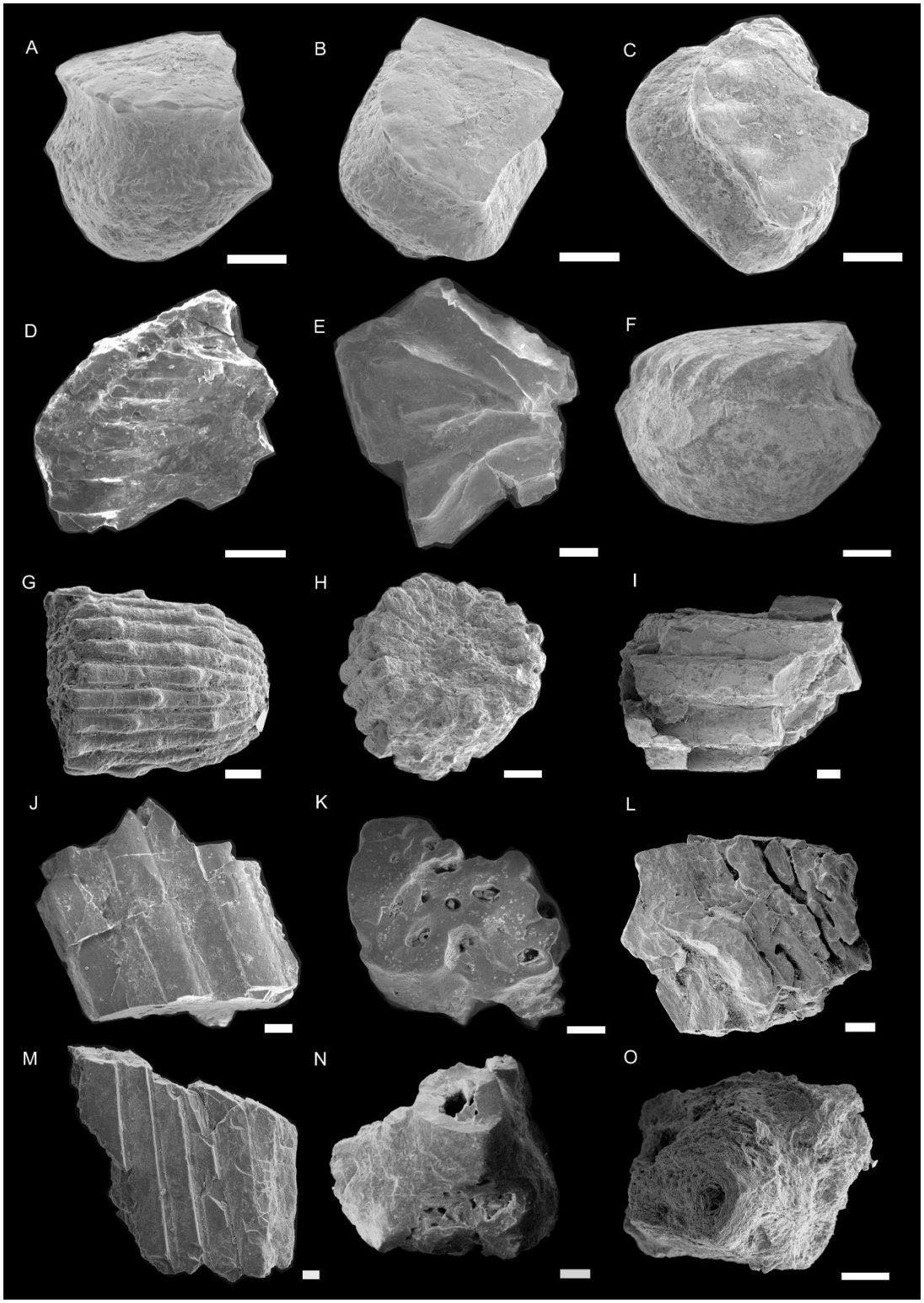
Description: Low flat scale with shallow base; crown rises rapidly from the base with distinctive ridges on edge. The second specimen (Plate 4.4, fig. E) has extensive ridges on the crown surface.

Remarks: Numerous fragments of acanthodian fin spine recovered could also belong to this taxon. However, due to their fragmentary nature, it is not possible to assign any of the fragments directly to *N. linleyensis* which is known from the DCSF (Miller and Märss 1999).



Text figure 4.12 Histology of acanthodian fin spines, in proximal view, found in in the DBB. A *Gomphonchus* sp. B-C *Onchus murchisoni* (Agassiz, 1837). cc central cavity, Mb missing bone, Sl superficial layer, Vc vascular cavity.

Plate 4.4



Explanation of Plate 4.4

Gomphonchus sp. A-B) WQ2a.212.G, C) DBB20.500.40, *Nostolepis* sp. D) DBB4.212.1, E) DBB5.500.h, indeterminate Acanthodii material F) DBB5.212.1, denticle. G) WQ1b.G, H) WQ1a1.212.H, I) DBB20.500.2, J) DBB4.500.2a, K) DBB.212.q, L) DBB5.500.1, M) DBB14.5.500.1, fin spine fragments. N) DBB19.500.5, O) WQ1a1.212.b tooth whorl fragments. A, F, G, I, L, M lateral view; B-D; oblique lateral view of the crown, E oblique lateral view, H, J; oblique lateral view of the tooth; tooth view O, K; dorsal view of fin spine. Scale bar represents 100 µm.

Genus ONCHUS Agassiz, 1837

Type species. Onchus murchisoni Agassiz, 1837, Ludlow Bone Bed, Shropshire U.K.

Onchus murchisoni Agassiz, 1837

Plate 4.5 Figure A-B Text Figure 4.12 B-C

1837 *Onchus murchisoni* Agassiz, p. 6, Tab. 1, figs 1, 2.
1853 *Leptocheles leptodactylus* McCoy p. 12.
1857 *Onchus murchisoni*; Egerton, p. 288, pl. 10 fig. 6a
2017 *Onchus murchisoni*; Newman et al. p. 455, fig. 3

Material: 1 pectoral-fin spine and one dorsal-fin spine in hand specimen, two thin sections.

Diagnosis (after Denison 1979): Fin spines are small, straight or slightly curved, laterally compressed, gradually tapering, and ornamented by usually smooth, broad, rounded longitudinal ribs. Denticles are absent on the posterior edge. The inserted base is typically short or absent. The middle layer has irregular longitudinal canals, and a subcostal canal is not developed below the anterior rib.

Description: DBBM 1 (Plate 4.5, fig. A) 21 mm long; proximal end bifurcates. Damage reveals the internal structure of narrow striations running parallel along the length of the spine. Along with the leading edge of the spine, the groove is present; the distal end of the spine tapers to point. DBBM 8 (Plate 4.5, fig. B) 27 mm long, spine broken along its length, distal end shows internal structure. Spine curves gently, with a vascular cavity at the distal end where the internal structure is exposed. The large groove runs along half of the total length from the proximal end to a medial point. The spine is larger and more elongate than those of *Gomphonchus* sp.

Histology: The superficial layer is also heavy crenulated as is seen in the macro specimens of *O. murchisoni.* The other key difference in morphology is that the

central cavity is open and not surrounded like that of the *Gomphonchus* sp. spine (Text-fig. 4.13 A)

Remarks: *Onchus murchisoni* is known only from fin spines and has been found in both the Ludlow and Temeside bone beds (Dineley and Metcalf 1999).

Class Acanthodii Owen, 1846

Order Incerti ordinis

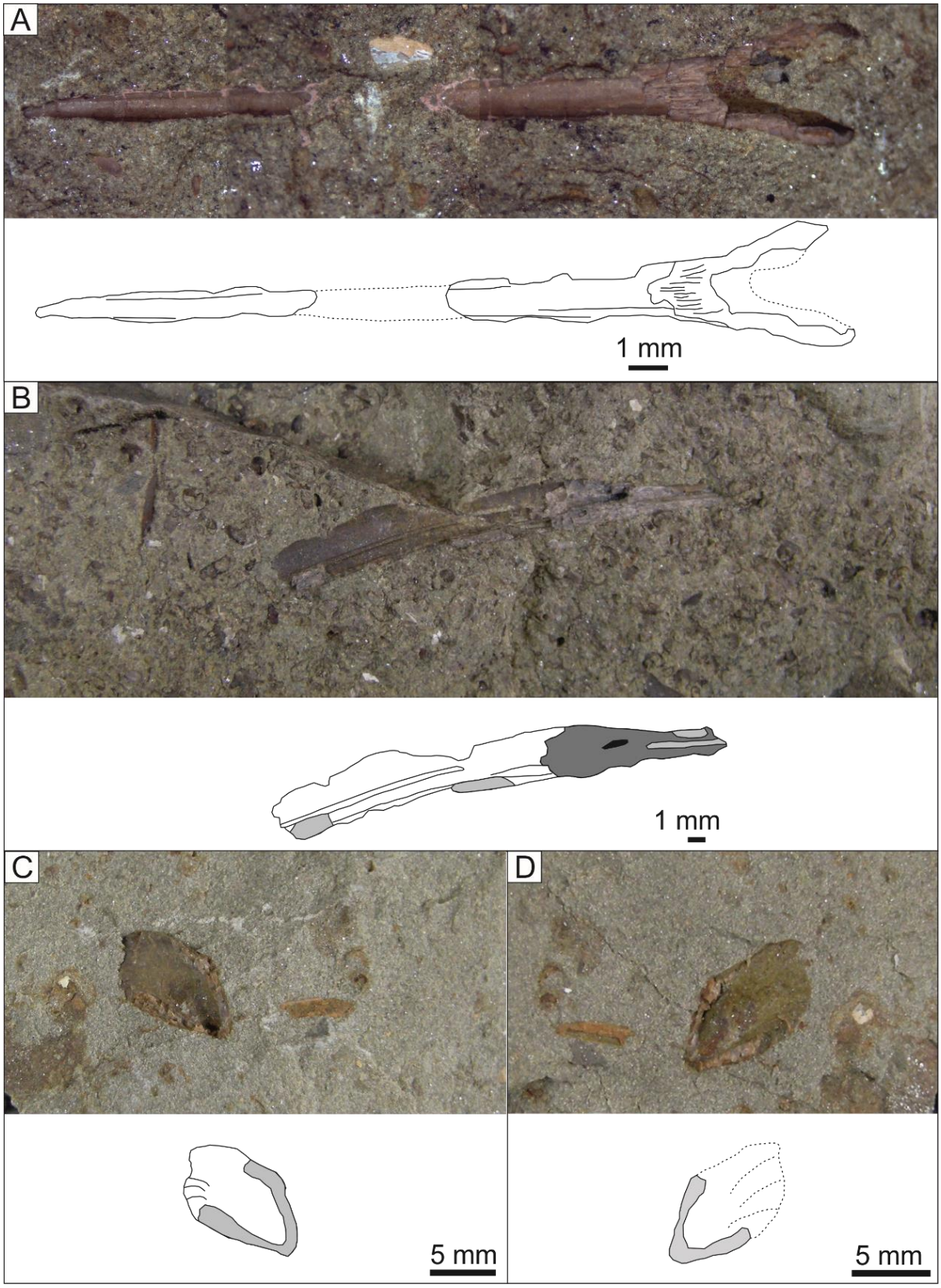
Family Incertae familiae

Material: 1 ventral fin spine, one denticle and 31 fragments of fin spines, one fin spine in thin section. Collected from the residues prepared from the DBB at Weir Quarry.

Description: The fin spine is 8.5 mm by 5 mm; it was exposed by splitting the rock. This resulted in the spine being split along a 45° angle showing the curvature tip of the spine in the sediment infill (Plate 4.5, fig. D), and the counterpart shows the spine with the outer edge showing crenulations with shallow ridges running to the point. The fragments show well-defined ridges. One fragment (Plate 4.4, fig. G) shows the characteristic “teardrop” structure seen on the fin spines.

Histology: Fin spine shows vascular bone histology (Text-fig. 4.12 A). Outer superficial layer shows no evidence of orthodentine. However, a thin dark line on the outer edge can be seen, possibly an oxidised film (Text-fig. 4.12 A).

Plate 4.5



Explanation of Plate 4.5

Macro specimens of acanthodian spines found in the DBB: A-B *Onchus murchisoni* (Agassiz, 1837); C-D indeterminate fin spine side and counter side Acanthodii fam., ord gen. et sp. indet? A) DBBM 1 lateral view B) DBBM 2 lateral view C) DBBM 12 dorsal view D) DBBM 13 dorsal view.

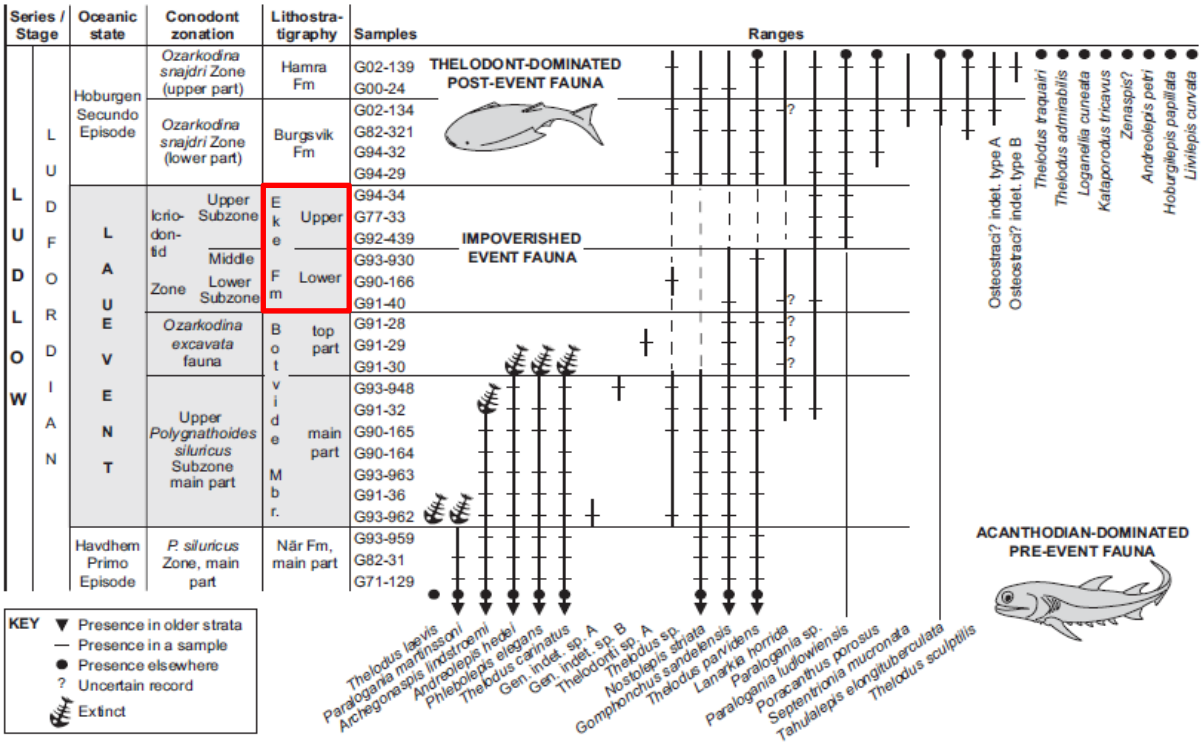
4.4 Discussion

4.4.1 Low faunal diversity

The main component of any bonebed is the vertebrates that it contains. They can offer insights into past ecosystems. When interpretations are made, time-averaging, and that bone beds often represent allochthonous deposits (Rogers and Kidwell 2007) must be considered.

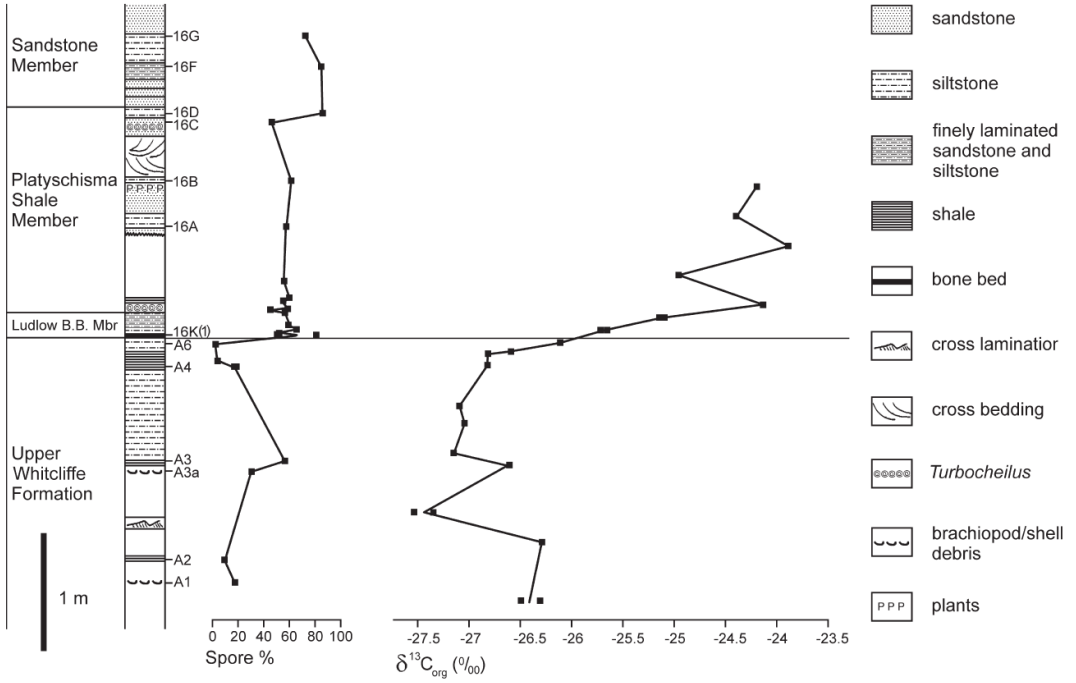
One of the most striking observations of the vertebrates from the DBB is that the overall diversity is low. There are only two thelodont genera present, *Paralogania* and *Thelodus*. The acanthodian fauna is slightly more diverse with as many as four genera if *Onchus* is included. Based on material published and recorded from other localities of the DBB it should be noted that the diversity of the DBB includes also two Osteostraci: *Sclerodus pustuliferus* and *Hemicyclaspis murchisoni* (Dineley and Metcalf 1999) and the heterostracan, *Archegonaspis* sp. (Miller 1995b).

While the environment itself can explain the low diversity, during the mid-Ludfordain, when the DBB was formed, there was a globally recognised event that may have had an impact on vertebrate life. The Lau Event, as described in chapter 1, is associated with, but precedes the most significant carbon isotope excursion (the Mid Ludfordian CIE) in the Phanerozoic. Having been correlated around the world (Märss 1992; Märss et al. 1998; Jeppsson 2012), workers have then been able to study vertebrate faunas through the excursion interval. One such study was carried out on the vertebrate extinctions and reorganisation of faunas in the late Silurian of Gotland (Eriksson et al. 2009). It was found that before the Lau Event the vertebrate fauna was dominated by acanthodians. Then, during the Lau Event, there was an impoverished fauna. Then, at the end of the Lau Event, the vertebrate fauna was dominated by thelodonts (Text-fig. 4.13), although shortly after the changed again during recovery.



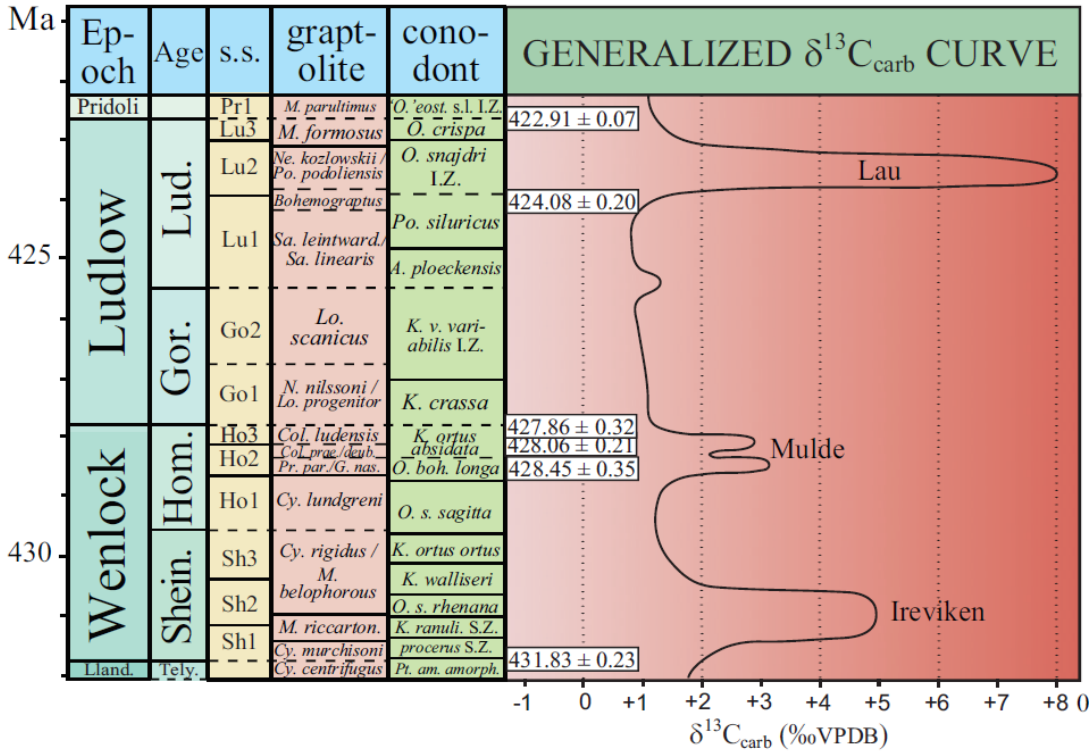
Text figure 4.13 Stratigraphical distribution of vertebrates during late Ludlow Lau Event. Only vertebrate-yielding samples are included in the chart. Dashed lines indicate Lazarus patterns, red box indicates positon of LBB, based on thelodont data from Loydell and Frýda (2011) (Modified from Eriksson et al. 2009).

The critical point of discussion, of course, is how does this relate to the DBB? It is first necessary to ascertain where the Lau Event is in relation to the DBB. Loydell and Frýda (2011) generated a carbon isotope curve from samples gathered at Weir Quarry (Text-fig. 4.14). The curve shows that the mid Ludfordian excursion appears to have begun before the LBB was deposited and that beds above including the DBB were laid down within the positive carbon isotope excursion. It is then possible to correlate the DBB with other formations globally (Text-fig. 4.15). On Gotland, the vertebrate fauna had already suffered from the effects of the Lau Event before the mid Ludfordian excursion commenced with many genera already extinct (Text-fig. 4.13) (Eriksson et al. 2009).



Text figure 4.14 Percentage spore abundance and $\delta^{13}C_{org}$ curves through the Upper Whitcliffe Formation and Lower Downton Castle Sandstone Formation exposed at Weir Quarry (SO 45607525), showing the rising limb of the Mid Ludfordian CIE through the LBB and subsequent beds (taken from Loydell and Frýda 2011).

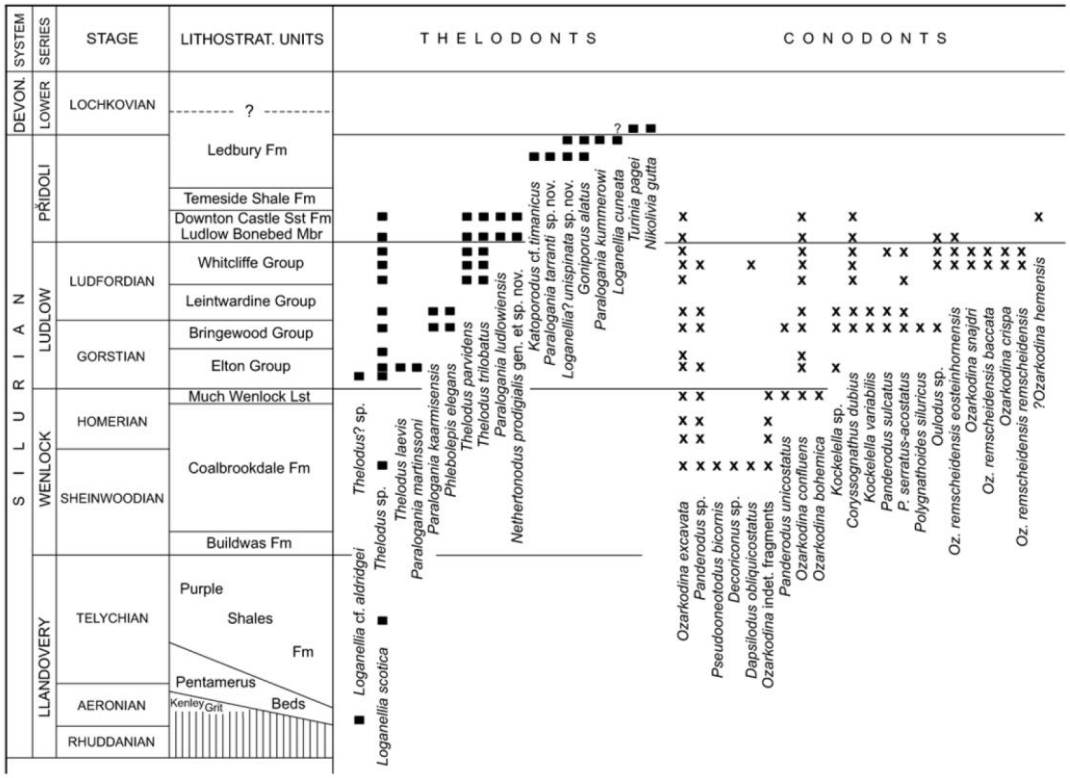
Although it would be easy to make a direct correlation between what is seen in the Eke Formation (the impoverished fauna shown in Text-fig. 4.13) and the DBB with its low diversity fauna, it is necessary to look first at what faunal diversity was below these levels in the Welsh Borders. A review paper on the distribution of thelodonts and conodonts in the Welsh Borderlands was produced by Märss and Miller (2004). Their findings are summarised in Text-fig. 4.16. Thelodonts are never particularly diverse in the Welsh Borderlands, being particularly rare in the Wenlock (Märss and Miller 2004). Conversely, they appear most diverse in the LBB and DCSF with five genera being present. However, this signal is most likely picking up on the fact that the bonebeds have condensed material over an extended period, giving the impression that the fauna was more diverse. It then makes it difficult to determine any signal that may be present in an ecosystem that is responding to a minor extinction event. To compare this faunal pattern a third deposit is considered here, the Arisaig Group, Nova Scotia. This is a useful deposit to compare with the DBB as it appears that the Moydart Formation was deposited contemporaneously with the lower part of the DCSF (Burrow et al. 2013).



Text figure 4.15 Silurian chronostratigraphic chart, indicating the position of the mid Ludfordain CIE (here refered to as the Lau CIE) and its duration (modified from Cramer et al. 2015).

The Arisaig Group, Nova Scotia (Burrow et al. 2013) has faunal diversity similar to that of the DBB with only rare thelodonts, acanthodians and conodonts being recorded (Burrow et al. 2013). Within the Moydart Formation, only one thelodont is recorded, *Paralogania ludlowiensis*, and one acanthodian, *Gomphonchus* sp. (Burrow et al. 2013). This diversity is lower than that seen in the Stonehouse Formation, which records two thelodont taxa, *P. ludlowiensis* and *Thelodus parvidens*, and five acanthodian taxa, including *Gomphonchus* (Burrow et al. 2013). This diversity in the Stonehouse Formation is close to the that of the DBB, as well having a similar fauna, with both thelodonts being recorded in the DBB along with some of the acanthodian taxa. The material recovered and described by Burrow et al. (2013) was not recovered from bonebed deposits, possibly suggesting that this was the fauna present without time averaging taking place. The age of the Stonehouse Formation is cited as being Přídolí (Burrow et al. 2013). This is based on the work of Melchin and Macrae (2005); however, in light of the faunal similarities, it may be that the Stonehouse Formation dates to the mid Ludfordain. It is unclear, however, whether the low diversity in the Moydart Formation is due to fewer samples being taken by Burrow et al. (2013) or reflects environment stress. The upper part of the

Moydart Formation has been suggested to have been deposited during the shallowing associated with the mid Ludfordian CIE (Burrow et al. 2013).



Text figure 4.16 Distribution of thelodont and conodont taxa over the Silurian and Lower Devonian of the Welsh Borders. The time scale for the Ludlow and Přídolí is now inaccurate (see Loydell and Frýda 2011) (taken from Märss and Miller 2004).

What is of particular interest is that unlike the Eke Formation of Gotland, which was deposited on the palaeocontinent of Baltica within a warm epicontinental sea (Bremer 2017), the Arisaig Group of Nova Scotia was deposited on the same palaeocontinent as the DBB on the western coast of Avalonia. Crucially it was deposited during the Lau Event, on the same continent but outside of the Downton Sea and not deposited within bonebeds, suggesting that during the late Silurian vertebrate faunal diversity was low elsewhere. It is not clear yet, however, if this was due to the effects of the Lau Event or if other factors could have led to this decrease in the diversity of the vertebrate fauna.

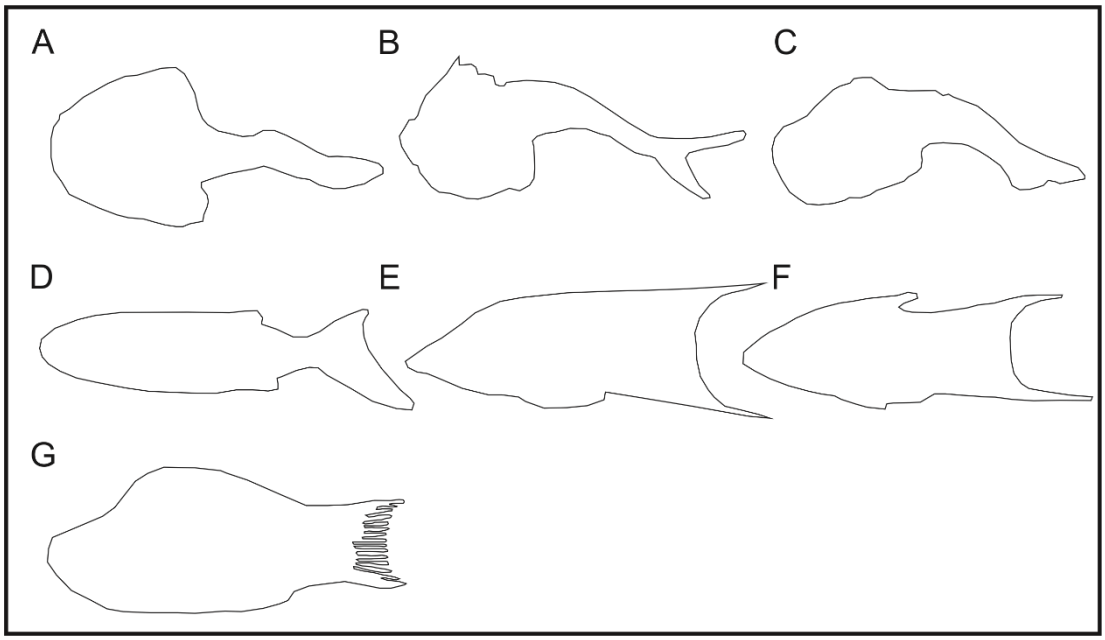
In summary, it is unclear whether the low faunal diversity seen in the DBB is due to the mid-Ludfordian Lau Event or due to other environmental factors. When looking at the published data on the LBB (Antia 1979; Dineley and Metcalf 1999; Märss and Miller 2004) and TBB (Antia 1980; Dineley and Metcalf 1999; Märss and Miller 2004), as well as the Arisaig Group (Burrow et al. 2013), it is clear that the vertebrate turnover seen in Gotland is not recorded in the Welsh borderlands and Nova Scotia (Avalonia), with thelodonts becoming scarce and acanthodians becoming dominant (Antia 1980; Dineley and Metcalf 1999). Of interest is the observation that in all three locations, the thelodonts *P. ludlowiensis* and *T. parvidens* are recorded, particularly *P. ludlowiensis*, suggesting that this taxon was thriving despite the environmental stresses, although *T. parvidens* does appear to have suffered a decline, in Gotland it disappears from the upper Eke Formation before returning. In Nova Scotia *T. parvidens* is missing from the Moydart Formation before being recorded in the Stonehouse Formation. In the Welsh Borderlands *T. parvidens* is also uncommon, being uncommon in the DBB compared to *P. ludlowiensis* and this also seen in the sample from Linley Brook above the DBB, where they are recorded as rare (Miller and Märss 1999). Further study is required to see more substantial evidence as there may be biases present, such as all of the Welsh Borderlands data coming from bonebeds.

4.4.2 Thelodont ecology

Environments in which thelodonts are found are varied and range from lagoons through to open shelf, slope and depressions (Märss and Einasto 1978, fig. 6; Märss et al. 2007, fig. 31). Evidence of thelodont diet comes mostly from looking at the body shape (Text-fig. 4.17) of articulated specimens and where they are found. The inference is that those with broad buccal cavities and flattened bodies were more suited to deposit-feeding, while others which have laterally compressed bodies with small buccal cavities could have been open shelf active swimming filter feeders (Märss et al. 2007). A recent study investigated thelodont ecology and squamation (Ferrón and Botella 2017) using the morphometrics of modern chondrichthyans and compared this to data collected on thelodonts. They suggest that a large number of thelodonts were demersal species inhabiting hard substrates like caves and cavities in reefs or rocky environments using their flexible micromeric armour to take

advantage of this environmental setting. They go on to suggest that only a few were demersal species inhabiting sandy or muddy substrates. Their data allowed them to suggest that there is evidence for universal schooling behaviour, and that scales also had defences against ectoparasites.

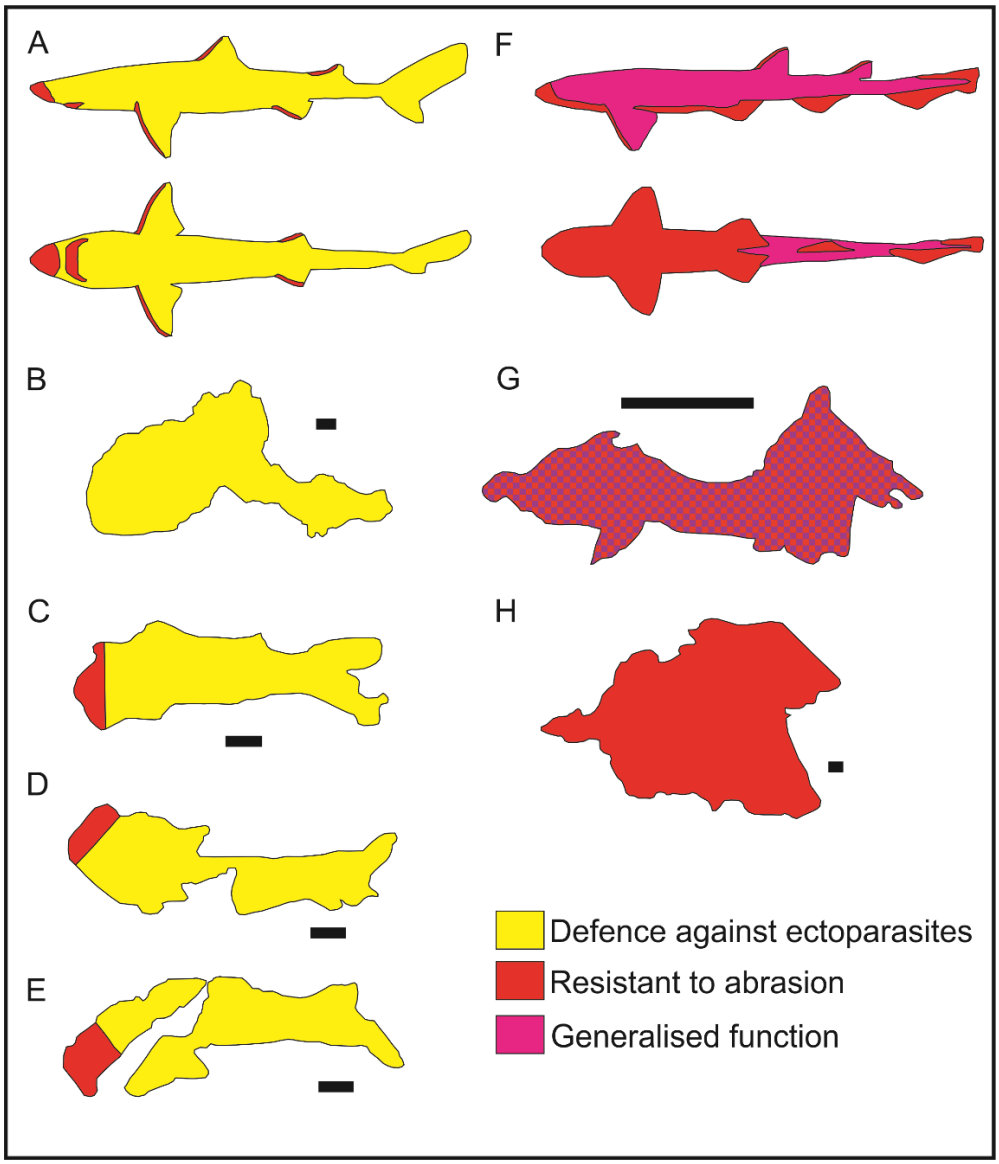
In many of the articulated thelodont specimens, the head region is covered in denticles adapted to cope with abrasion. This pattern could suggest that these thelodonts (Text-fig. 4.18) were deposit-feeding, possibly living above a sandy bottom. It could be inferred that perhaps some taxa were feeding on sandy substrates, but if a predator appeared, they might have retreated to a reef or rocky shore to hide among the rocks or partially bury themselves in the sediment some as modern fish do.



Text figure 4.17 Selection of thelodont body forms (modified from Ferrón and Botella, 2017): A, *Turinia pagei* in dorsal view. B, *Lanarkia horrida* in dorsal view. C, *Loganellia scotica* in dorsal view. D, *Phlebolepis elegans* in lateral view. E, *Sphenonectris turnerae* in lateral view. F, *Furcacauda heintzae* in lateral view. G, *Pezopallichthys ritchiei* in lateral view (Original outlines, A, B and C Märss & Ritchie 1998; D from Ritchie 1968; E, F, G modified from Wilson & Caldwell 1998).

How do these data infer an ecology for the two taxa present in the DBB? *Paralogania ludlowiensis* and *Thelodus parvidens* are found in various deposits around the northern hemisphere from both the palaeocontinent of Avalonia and Baltica (Märrs et al. 2007). *Paralogania* is known only from isolated denticles (Märss et al. 2007). However, it is nested within the family Shieliidae (Wilson and

Märss, 2009). Also in Shieliidae is the genus *Shielia* (Märss and Ritchie 1998) which is known from articulated material and is featured as part of the Ferrón and Botella (2017) study. They looked at three species of *Shielia* all showing the same denticle function. Their bodies are covered in denticles suited for defence against ectoparasites while their heads are covered in denticles that are more suited to resisting abrasion. This distribution of denticles could suggest that they required a form of protection from abrasion around their heads, possibly implying that this taxon was engaging in such an activity (i.e. deposit-feeding) that required resistance to abrasion. When compared to modern chondrichthyans that have this same pattern of denticle covering, Ferrón and Botella (2017) noted that only one of the sharks had this same configuration, *Squalus acanthias* (spiny dogfish). This shark is a demersal species that is commonly found at depths of around 50–150 m but has been reported in water deeper than 700 m (Castro 2010). Due to *Paralogania ludlowiensis* being in the same family (Shieliidae), it is inferred here that *P. ludlowiensis* was also a demersal species that possibly had a schooling behaviour.



Text figure 4.18 Patterns of denticle coverage and their function on the two closest taxa to *Paralogania ludlowiensis* (B-E) and *Thelodus parvidens* (G-H). Also included are the two modern analogues for the ecology that their squamation suggests. A, Schooling species of low to moderate speed (illustrated by *Squalus acanthias*). B, *Shielia gibba*. C, *Shielia parca*. D-E, *Shielia taiti*. F, Demersal species on sandy and muddy substrates (illustrated by *Scyliorhinus canicula*). G, *Thelodus laevis*. H, *Thelodus macintoshi*. Scale bars represent 1cm; modified from Ferrón and Botella (2017).

Thelodus parvidens is also known mostly from isolated denticles. However, some partially articulated material has been attributed to *Thelodus parvidens* (Turner 1986), originally thought to be the remains of *Thelodus macintoshi* (Stetson 1928). Ferrón and Botella (2017) include *Thelodus macintoshi* in their data set, although herein this material will be considered with caution as Turner (1986) discussed how *T. macintoshi* is heterogeneous, with the specimen being made up of several different

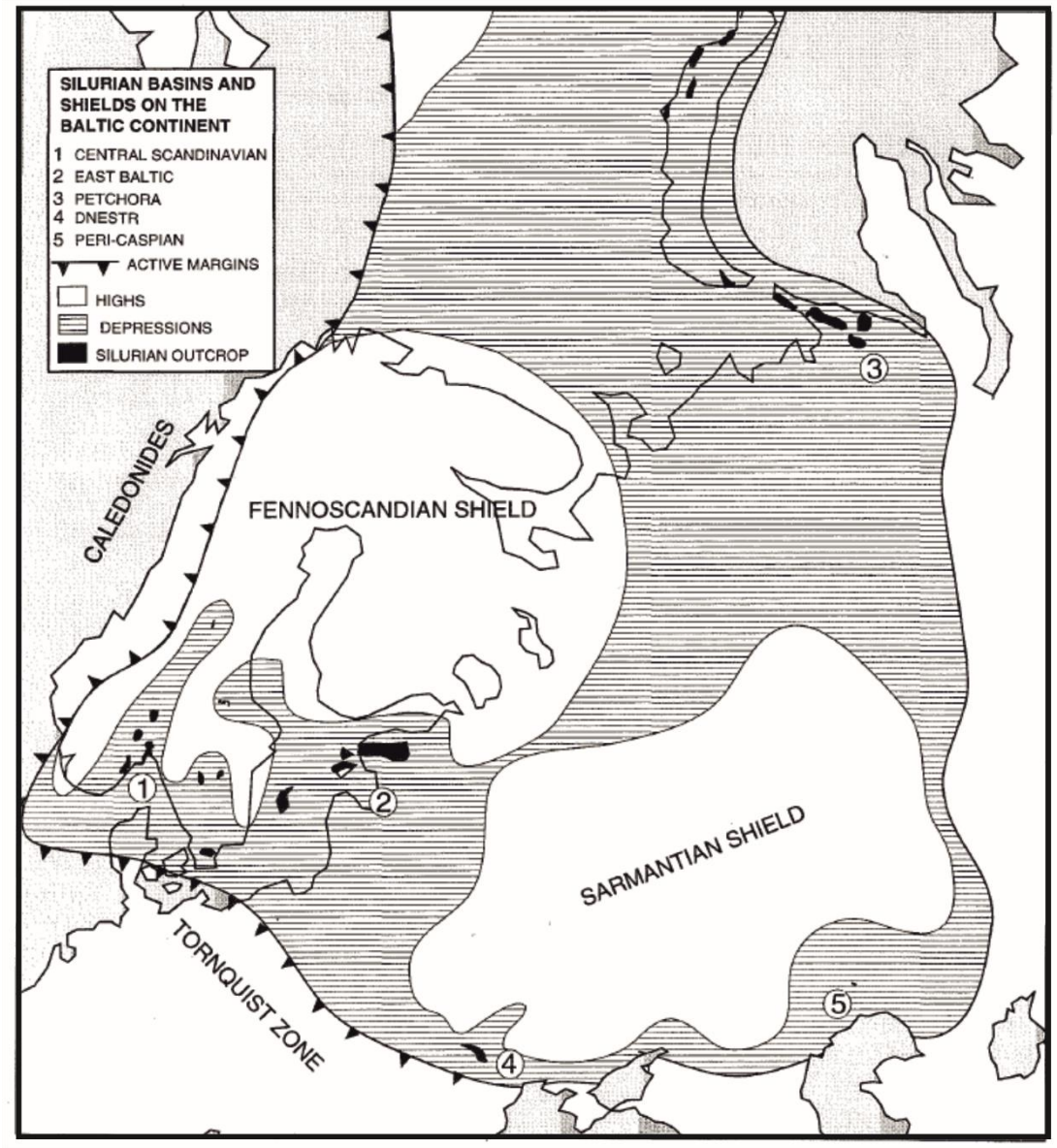
genera and even classes. Turner found that numerous specimens that had been initially assigned to *T. macintoshi* were in fact from different taxa. For example, the holotype of *T. macintoshi* (MCZ 2035) was reassigned to *T. parvidens*. It is this specimen that is illustrated in Ferrón and Botella (2017, fig. 6 D') and this study (Text-fig. 4.18, H). Obviously the data collected for the holotype of *T. macintoshi* (MCZ 2035) can be used for *T. parvidens* as they are the same species. The specimen that Ferrón and Botella show does seem to be covered in abrasion-resistant denticles. The other *Thelodus* species used by Ferrón and Botella is *T. laevis*. Its denticle functionality is less clear as it has coverage of both generalised and abrasion-resistant denticles; however, Ferrón and Botella (2017) suggest that thelodonts with this pattern are similar to the sharks that are demersal and inhabit a muddy/sandy bottom. Comparisons can be made with *Scyliorhinus canicula* (small-spotted catshark) which can be found at depths of only a few metres up to 400 m (Rodríguez et al. 2007).

Paralogania ludlowiensis would have been the more common thelodont in the ecosystem with the larger (Turner 1986) *Thelodus parvidens* being rarer as is shown by the differences in abundances (Antia 1980; Märss and Miller 2004; Eriksson et al. 2009; Burrow et al. 2013). Although, as discussed above, interpreting the ecology of an organism that can move around an ecosystem is problematic, an attempt to do this has been made to establish palaeocommunities based on thelodonts, due to their abundance in the Silurian and Lower Devonian. Turner (1999) suggested that *Thelodus parvidens* is often found in association with *Paralogania ludlowiensis*. The palaeocommunity that Turner proposed that is most relevant to the DBB was the *Thelodus parvidens* community. This palaeocommunity has many similarities with the DBB fauna. The composition of the community is like that of the DBB except for the abundance of other species of the genus *Thelodus* as only *T. parvidens* is recorded from the DBB, but the presence of acanthodians, lingulid brachiopods and ostracods is consistent. The age and type locality are also consistent with the DBB. Possibly though, the most intriguing aspect of her palaeocommunities model is the geographical distribution which she suggests is the Anglo-Welsh border, Eastern Canada, Norway, Southern Sweden, Beyrichienkalk, Baltic Countries and North Timan, all of which are geographically close during the mid-Ludfordian (Text-fig. 4.20) except for North Timan which appears to be in isolation. It should be noted that

there are no *T. parvidens* known from Norway and the Beyrichienkalk is material from glacial till (Märss pers. comm. 2019). The localities plotted in Text-fig. 4.19 show that all of these palaeocommunities were deposited in shallow seas, which may have been interconnected or at least possible for fauna to move between. This observation supports Turner's (1999) proposal, as it demonstrates that these communities could have been geographically linked. However, this does not explain the North Timan locality which would appear to be isolated from the other communities. Baarli et al. (2003) presented an alternative palaeogeographical reconstruction which would allow for this shared community. They suggested that Baltica was not one but three separate islands with depressions between them allowing for the continuation of shallow seas from Scandinavia to North Timan (Text-fig. 4.20) and this supports the inference of the thelodonts and acanthodians being cosmopolitan at a generic level during the late Silurian.

Ferrón et al. (2018) suggest that the spatial distributions of some thelodonts, including *Paralogania ludlowiensis,* is evidence of diadromous lifestyles. Being located near to fluvial and marginal marine environments may explain why they are consistently seen in the shallow seas of what is now the northern hemisphere. To support this idea of a thelodont community, it has been suggested that thelodonts may have had a pelagic larval stage (Ferrón et al. 2018) This also would have allowed them to have spread along the shallow seas of Nova Scotia, the Welsh borderlands, the Baltic and Scandinavia.

Text figure 4.19 Palaeogeographical map with the locations of the *Thelodus parvidens* communities (Turner 1999), illustrating the ability for the community to spread across the region. CF Caledonian front; TS, Thor suture; IS, Iapetus Ocean suture (Modified from Torsvik and Cocks 2016).



Text figure 4.20 Figure 1 from Baarli et al. (2003); their interpretation of the Baltica continent during the middle Silurian.

5. Invertebrate palaeontology

5.1 Introduction

This chapter focuses on the invertebrates of the DBB at Weir Quarry. The chapter will describe previous work that is of relevance to this study and will comment on the preservation of the material. Descriptions of all the invertebrates found in the DBB at Weir Quarry are provided in the style of the journal *Palaeontology*. Finally, there will be a discussion on the findings of this chapter.

5.1.1 Previous work

Specific research on the invertebrate fossils of the DBB is limited. However, considerable work on invertebrates from the Ludlow Series of the Welsh Borderlands has been carried out over the last 175 years. Indeed, when the LBB was first discovered, many workers regarded the fish fossils with their shiny black appearance as fragments of crustaceans or other invertebrates. This confusion was touched on in the previous chapter with the discussions between M'Coy and Murchison.

The first significant work was Murchison's *Silurian System* (1839) in which Sowerby described a range of invertebrates including bivalves and gastropods as well as the brachiopod *Lingula cornea*. Later workers continued to study the invertebrates of the DCSF in the Welsh Borderlands. One group that received attention early in the history of research was the eurypterids: Salter (1852) provided a description of *Pterygotus problematicus*. Murchison (1859) described more invertebrate taxa in '*Siluria*'. This research was followed by several papers that added to scientific knowledge of late Silurian Welsh borderland invertebrate taxa including Harley (1861) who discussed the presence of crustaceans in the LBB; and Brodie (1869) who described the occurrence of *Eurypterus* and *Pterygotus* in the upper Silurian rocks of Herefordshire.

Elles and Slater (1906) carried out an extensive study on the geology of the upper Silurian of the Ludlow district; however, they only mention the invertebrate fossils and include faunal lists at the end of the paper (Text-fig. 5.1 and Text-fig. 5.2), which importantly have a specific column for the "*Platyschisma*-Bed" which

included what is now known as the DBB. The *Platyschisma* beds would eventually form the second member of the DCSF (the Platyschisma Shale Member or PSM). It was named for the fact that previous workers had found large quantities of the gastropod *Platyschisma helicites* (now known as *Turbocheilus helicites*) within the strata. Stamp (1918), who looked at late Silurian rocks in the Clun Forest area, also included a faunal list of invertebrate taxa found within the DCSF in that area. Cowper Reed (1934) described three localities in Worcester from which he described *Modiolopsis complanata*. King (1934) described the geology and palaeontology of the Downtonian and Dittonian of Great Britain focusing on the West Midlands of the U.K. He refered to the presence of *Modiolopsis complanata* as well as *Lingula cornea* and *Lingula minima*; however, he also provided an extensive faunal list. Earp, (1938) focused on sedimentology and lithostratigraphy but included a faunal list indicating which of the listed fossils are very common, common and rare.

VII. Fossil Lists.

[These lists are compiled from our own collections, supplemented by that of the Ludlow Museum.]

r = rare.
c = common.
C = very common.

	Aymestry Group.		Upper Ludlow Group.				Temeside Group.									
	Conchidium-Limestone.	*Dayia*-Shales.	*Rhynchonella-nucula* Beds.	*Chonetes*-Beds.	*Spirifera-elevata* Beds.	Ludlow Bone-Bed.	Mottled Beds.	*Platyschisma*-Bed.	Massive sandstones.	Carbonaceous sandstones.	Thinly-bedded sandstones.	Variegated rubbly shales.	Micaceous grit.	Olive shales.	Temeside Bone-Bed.	'Fragment-Bed.'
Brachiopoda.																
Lingula cornea, Sow.	...	...	...	...	...	...	...	...	...	...	...	c	c	C	c	c
L. lata, Sow.	c	c														
L. Lewisii, Sow.	...	...	c	C	c	r										
L. minima, Sow.	...	...	...	...	...	r	r	c	C	c	r	r				
Orbiculoidea rugata, Sow.	...	...	?	C	c	r										
O. striata, Sow.	...	...	r	r	r	r										
Crania implicata, Sow.	...	...	r	r	C											
Pentamerus (Conchidium) Knightii, Sow.	C															
Strophomena euglypha, His.	C	c														
Str. rhomboidalis, Wilck.	C	c														
Str. ornatella, Salter	C	c														
Orthis orbicularis, Sow. / *O. canaliculata*, Lindstr.	C	C	c	c												
O. lunata, Sow.	C	C	C	c	c	r										
O. cf. *elegantula*, Dalm.	c	c	c	c	c	r										
Atrypa reticularis, Linn.	C	C														
Chonetes minima, Sow.	...	...	r	r	r											
Ch. striatella, Dalm.	...	...	c	C	C	c										
Ch. lepisma, Sow.	...	...	r	r	r											
Rhynchonella nucula, Sow.	...	r	C	c	c											
Rh. (Wilsonia) Wilsoni, Sow.	C	c	r													
Dayia navicula, Sow.	r	C														
Spirifera elevata mut., Dalm.	...	...	...	r	C											
Whitfieldella didyma, Dalm.	C	c														
Lamellibranchiata.																
Avicula Danbyi, M'Coy	r	r	r	r												
Cucullella antiqua, Sow.	...	...	...	r												
C. coarctica, Phill.	r	r														
C. ovata, Sow.	r	r	r													
C. sp.	...	r	r	r	r											
Ctenodonta sp.	...	...	r													
Goniophora cymbæformis, Sow.	...	...	C	C	C											
Modiolopsis complanata, Sow.	...	...	...	...	...	...	...	C	Various small undeterminable Lamellibranchiata.							
M. lævis, Sow.	...	...	...	c	c											
M. mytilimeris, Conrad	...	...	...	c												
M. sp.	...	...	r													
Orthonota amygdalina, Sow.	r	...	...	C	c	r										
O. amygdalina var.	...	...	...	c	c											
O. angulifera, M'Coy	...	...	...	c												
O. impressa, Sow.	...	...	...	c												
O. rigida, Sow.	...	...	...	c												
O. semisulcata, Sow.	...	...	...	c												
O. solenoides, Sow.	...	...	...	c	c											
Pterinea hyans, M'Coy	...	...	c													
Pt. orbicularis, M'Coy	r	r														
Pt. retroflexa, Wahl	...	...	C	C	C											
Pt. tenuistriata, M'Coy	r	r														
Gasteropoda.																
Bellerophon expansus, Sow.	r	r	c	c												
B. Murchisoni, d'Orb.	...	...	...	r	r											
B. wenlockensis, Sow.	c															
Cyclonema corallii, Sow.	...	r	r	r												
Holopella gregaria, Sow.	...	...	...	...	...	r	...	c								
H. obsoleta, Sow.	...	...	r	r	r											
H. sp.	...	...	...	r												
Murchisonia articulata, Sow.	...	...	...	c												
Platyschisma helicites, Sow.	...	...	...	...	...	...	...	C								

Text figure 5.1 Faunal list produced by Elles and Slater (1906): red box indicates the fauna associated with the *Platyschisma*-Bed which included the DBB.

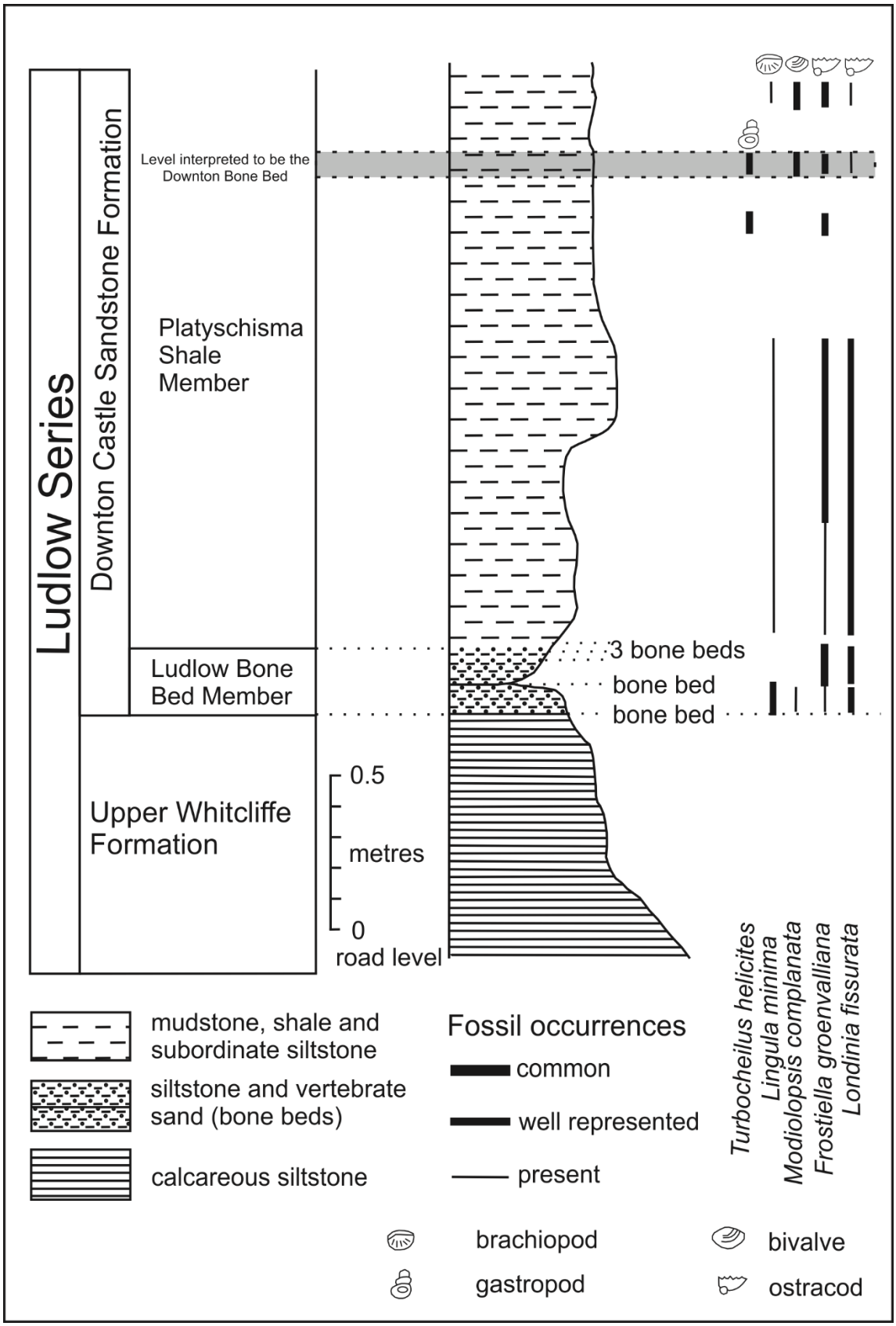
FOSSIL LISTS (*continued*).

r = rare.
c = common.
C = very common.

	Aymestry Group.		Upper Ludlow Group.					Temeside Group.								
	Conchidium-Limestone.	*Dayia*-Shales.	*Rhynchonella-wenlockia* Beds.	*Chonetes*-Beds.	*Spirifera-elevata* Beds.	Ludlow Bone-Bed.	Mottled Beds.	*Platyschisma*-Bed.	Massive sandstones.	Carbonaceous sandstones.	Thinly-bedded sandstones.	Variegated rubbly shales.	Micaceous grit.	Olive shales.	Temeside Bone-Bed.	'Fragment-Bed.'
CEPHALOPODA.																
Orthoceras bullatum, Sow.	...	...	c	C												
O. gregarium, Sow.	...	...	c	C												
O. ludense, Sow.	...	...	c	c												
O. sp.	...	...	...	c	c											
Lituites ibex, Sow.	...	...	...	c												
ACTINOZOA, etc.																
Chætetes sp.	...	...	...	c												
Aulopora serpens, Linn.	C	c														
Favosites Forbesi, M.-Edw.	C	c	c	c												
Stenopora fibrosa, Goldf.	c	c	c	c	c											
Spongarium Edwardsii, Murch.	C	c														
VERMES.																
Cornulites serpularis, Schloth.	...	...	...	c	c											
Serpulites longissimus, Murch.	...	...	c	c												
Spirorbis Lewisi, Sow.	...	...	...	r												
Trachyderma coriaceum, Phill.	...	...	c	c												
PLANTÆ (?)																
Pachytheca sphærica, Hooker	...	...	...	r	r	...	...	c	C	...	...	...	...	C	C	C
CRUSTACEA.																
Calymene Blumenbachii, Brong.	c	r														
Encrinurus punctatus, Brünn.	c	r	r													
Homalonotus Knightii, König	...	...	...	C	c											
Phacops sp.	...	...	...	...	c											
Eurypterus acuminatus, Salt.	...	...	...	...	r	...	...	...	...	...	...	...	...	r		
Eur. linearis, Salt.	...	...	...	...	r											
Eur. pygmæus, Salt.	...	...	...	...	...	...	...	...	...	...	...	...	...	c		
Eur. megalops, Salt.	...	...	...	...	...	...	...	...	...	...	...	...	...	c		
Eur. spp. various	...	...	...	r	...	r	...	...	c	...	...	c				
'*Parka decipiens*' (eggs)	...	...	...	...	...	...	...	...	...	...	...	...	c	c		
Pterygotus Banksii, Salt.	...	...	...	...	...	r	...	c	...	...	...	...	...	c		
Pt. gigas, Salt.	...	...	...	...	...	...	...	...	r	...	...	...	...	c	c	
Pt. ludensis, Salt.	...	...	...	...	...	...	...	...	...	...	...	...	...	c	c	?
Pt. problematicus, Ag.	...	?	r	r	r	r	...	r	c	...	...	...	...	c	c	?
Beyrichia Klædeni, M'Coy	...	...	C	C	C	...	r	C	c	c	c	c	c	c	c	
B. sp.	...	...	...	c	c	r	...	C								
Leperditia marginata, Keys.	...	...	...	...	...	...	...	...	...	...	...	c	...	c	...	c
L. phaseolus, var. *gracilenta* (Jones)	...	...	...	...	...	...	...	...	...	...	...	...	...	r		
L., small species	...	...	...	...	c	c	...	...	...	...	...	c	...	c		
Physocaris vesica, Salt. ?	...	...	...	...	...	...	...	...	...	...	...	...	...	c	c	
PISCES.																
Auchenaspis Salteri, Egerton	...	...	...	...	...	...	...	...	...	...	...	...	...	r		
Cephalaspis Murchisoni, Egert.	...	...	...	...	...	?	...	...	...	...	?	...	...	r	r	
Climatius	...	...	...	...	...	...	...	...	...	...	r					
Ctenacanthus	...	...	...	...	...	...	...	...	...	...	...	r	...	r	r	
Eukeraspis pustulifera, Ag.	...	...	...	...	...	...	...	...	...	...	c					
Hemiaspis	...	...	...	...	...	...	...	...	...	...	...	...	...	...	r	
Onchus Murchisoni, Ag.	...	...	...	...	...	c	...	c	...	...	...	r	...	c	C	r
O. tenuistriatus, Ag.	...	...	...	...	...	c	...	c	...	...	r	r	...	c	C	r
Thelodus parvidens	...	...	...	...	...	...	...	r								
Fish-spines	...	...	...	...	...	c	...	...	...	...	c					

Text figure 5.2 Faunal list produced by Elles and Slater (1906): red box indicates the fauna associated with the *Platyschisma*-Bed which included the DBB.

An important work on the eurypterids of the upper Silurian was that by Kjellesvig-Waering (1961) which reappraised many of the Anglo-Welsh eurypterid taxa. Further study of the Ludlow strata of the Welsh Borderlands was carried out by Holland et al. (1963); this updated the knowledge of the key invertebrate fossils that occur in the DCSF. Later papers have looked at the distribution of Silurian microfossils (Aldridge et al. 1979) of which the ostracods are of relevance here. Bassett et al. (1982) contains lists of fossils found within the "Downton [now Přídolí] Series". This paper was one of the first to use what would be regarded as modern stratigraphical nomenclature and thus puts the fossils into a modern lithostratigraphical context. Within the PSM (although not referred to by name) they record the following: *T. helicites*, which they state is common near the base; *M. complanatus* (most likely an error and they meant *Modiolopsis complanata*) is also recorded near the base along with *Frostiella groenvalliana* and *Londinia fissurata* the occurrence of which coincides with locally developed bonebeds. They also mention several eurypterid taxa, which are recorded as being common. Siveter et al. (1989) provided a field guide to major geological locations across the Welsh borderlands. However, it is their modified figure 38 (Text-fig. 5.3) originally by Bassett et al. (1982) that is of interest as it shows invertebrate occurrences across the then Ludlow-Přídolí boundary. Another key summary of Silurian invertebrates is in *A global standard for the Silurian System* (Holland and Bassett 1989) which provides an overview of the major groups of invertebrates but nothing specifically on the beds associated with the DBB.



Text figure 5.3 The lithological and faunal succession from locality 3.2b on the N side of Whitcliffe Road, Ludlow (modified from fig. 38 in Siveter et al. 1989). Approximately 1.5 m above the base of the LBBM is an assemblage that appears to be an indicator of the DBB.

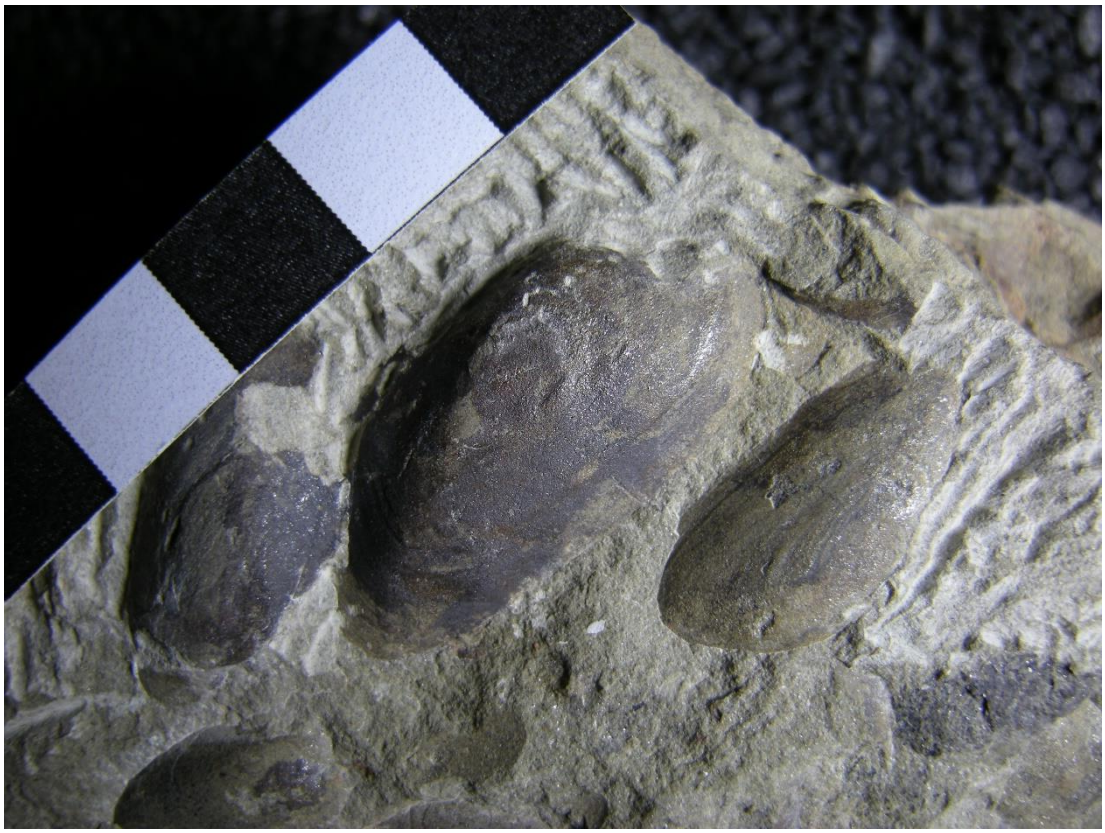
Miller (1995a) looked at the distribution of ostracods and conodonts across the Ludlow/Přídolí boundary, taking in the same strata that contain the DBB as well as Weir Quarry. Later Miller et al. (1997) described the microfossil and sedimentary strata near Clun in Shropshire.

It was not until the mid-1990s that the most significant group of invertebrates was found. Jeram et al. (1990) reported the discovery of cuticle from a trigonotarbid, later described by Dunlop (1996) as *Eotarbus jerami,* later renamed *Palaeotarbus jerami* (Dunlop 1999). Dunlop (1996) made it clear that the precise horizon that the specimen came from is unknown; however, he suggested that the horizon with the richest organic deposits is 1.6 m above the basal Ludlow Bone Bed Member, within the Platyschisma Shale Member. *Palaeotarbus jerami* may be the oldest known terrestrial animal (Suarez et al. 2017). Work has continued on the Silurian invertebrates of the Welsh Borders. Of note is the eurypterid work by Tetlie (2006, 2007) once again reappraising the eurypterids of the Welsh Borders. An important paper has also been published on the brachiopods of the upper Silurian. Cocks and Popov (2009) provided a reappraisal of the linguloid brachiopods. Although research has not stopped on these groups, it has been a considerable amount of time since a paper discussing the key DBB taxa or the DCSF invertebrates has been published.

5.2 Preservation and taphonomy

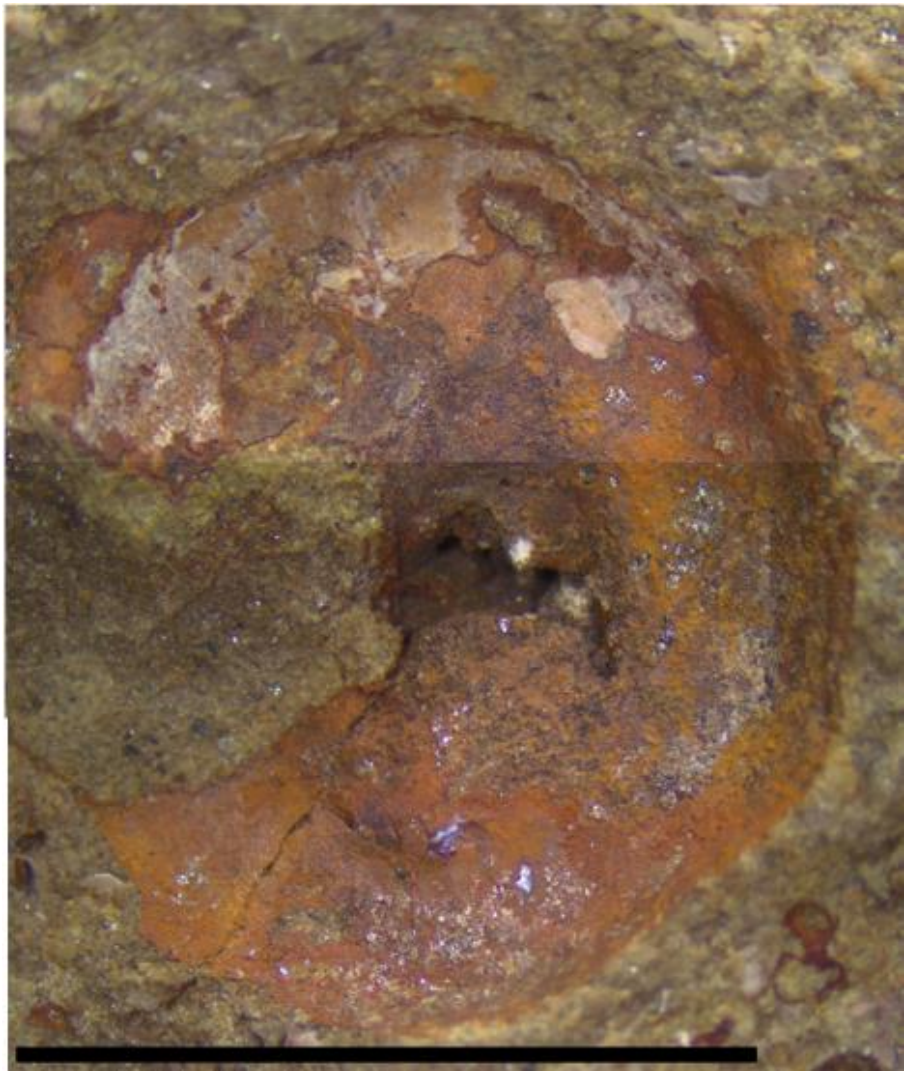
5.2.1 Preservation

The preservation of the invertebrates within the DBB is varied, because of the various mineralogies that make up the organisms' shells and other skeletal remains. The only bivalve known from the DBB, *Modiolopsis complanata*, appears to have had an aragonite shell (Harper et al. 1997). Aragonite is metastable and in early diagenesis is often replaced by calcite; as a result, there are no aragonite shells preserved from before the Carboniferous (Runnegar 2008). However, within the DBB, even the calcite that probably replaced the original shells of the *M. complanata* has been lost during diagenesis. Many of the shells are internal moulds with no internal detail preserved except for growth lines. They exhibit a dark, possibly oxidised surface (Text-fig. 5.4).



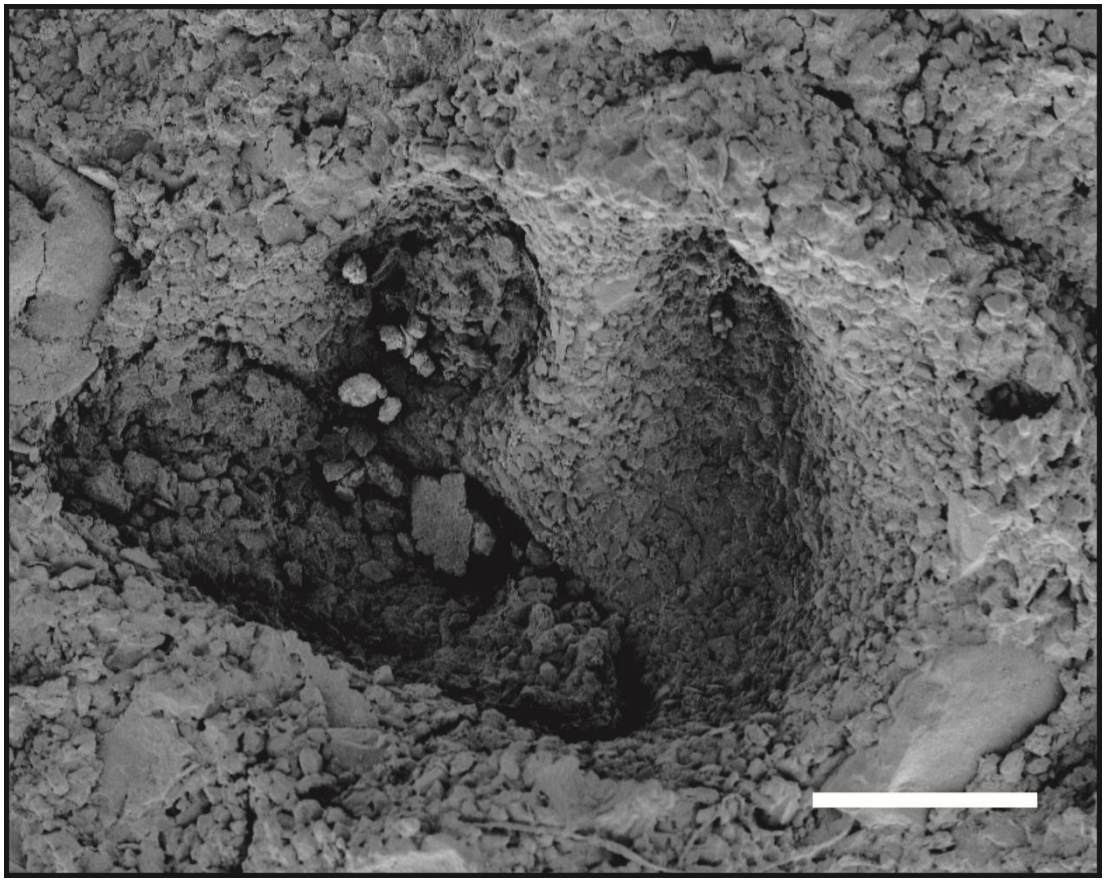
Text figure 5.4 *Modiolopsis complanata*: close-up of specimen DBBM3; growth lines can be seen across the oxidised surface. The scale is 1 cm per division.

The gastropod found within the DBB, *Turbocheilus helicites*, is preserved similarly to *M. complanata*, as moulds often with an oxidised appearance. One specimen, however, DBBM4 (Text-fig. 5.5) shows what may be part of the shell. This may be some of the original shell, replaced by calcite, or this may be a cast.



Text figure 5.5 Close-up of *Turbocheilus helicites* DBBM4, note the white/cream coloured material at the top of the image, possible preservation of shell. Scale represents 1 cm.

The ostracods within the DBB are also preserved as moulds with the original calcite valves dissolved away (Text-fig. 5.6). Some show a dark outline in cross section. Of interest is that using the paraffin expansion method (Hauser 2016), some ostracods were liberated from the host rock. The sediment grains adhered together, forming the internal mould. Identification to generic level was made with confidence; however, as the moulds are formed of coarse sediment grains, they do not record finer details of the valves.



Text figure 5.6 External mould of *Londinia arisaigensis* (Copeland 1964) showing a possible brood pouch. Scale bar represents 500 µm.

The other common invertebrates seen in the DBB are the brachiopods, *Tunisiglossa cornea* and *Lingula missendenensis*. These, are preserved as the original shell. This is due to these brachiopods being lingulates which have shells of calcium phosphate. They are often found as fragments although there are also examples of near-complete specimens from the DBB.

Although eurypterids are present, it is only as fragments. Eurypterid exoskeleton is a cuticle similar in structure to that of modern arthropods (Dalingwater 1973), and the material found in the DBB has a black, almost carbonised appearance.

5.2.2 Taphonomy

The DBB bivalves and gastropods are found associated with the vertebrate material within the bed itself. The bivalves do not show any preferred orientation (Text-fig. 5.7), which might indicate that at time of deposition there was no specific flow direction which might have produced a stringer or preferred orientation. Further, although the valves have been lost through diagenesis, they are complete but disarticulated. This means that when the valves were deposited, they were complete. It is unclear, however, what state the valves were in at time of deposition; despite being complete, the amount of boring, corrasion, and encrusting information has been lost. It is also unclear for how long or to how much energy the valves were exposed to before deposition.
The three gastropod specimens are preserved in a similar mode to the bivalves; they are all found with the apertures facing down (Text-fig. 5.8). It is unclear how complete some of the gastropods were at the point of deposition as they are preserved as internal moulds.

The preservation of the brachiopods, is as their original shell. There are two main modes of preservation: the first and most common mode is that the brachiopod is fragmented; some of the fragments show sharp edges while others are rounded (Plate 5.1). This difference could be due to some of the fragments being exposed for a more extended period, allowing them to be abraded before being deposited. It could be suggested that fragments with the sharp edges are a result of the preparation of, and extraction of the fossils. Far less common than the fragments, are near complete

specimens (Plate 5.1). The brachiopods show similar taphonomy to the *Paralogania ludlowiensis* denticles, showing a contrast between near-complete specimens and weathered fragmented material. This suggests that two different events took place. First the brachiopods, possibly post-mortem shells, were exposed on the seabed and as a result of current action were broken and fragmented. This could also be due to the material being reworked from earlier deposits. The other event would appear to have been just before the deposition of the DBB. As the modern *Lingula* is infaunal in its life habits, and the shape of their shells are similar, it could be inferred that the lingulids in the DBB were living within sediment when a high energy event picked them up and deposited them in the DBB. This also supports the concept that the DBB is an allochthonous deposit.

The taphonomy of the ostracods is similar to that seen in the bivalves; the valves are disarticulated (Text-fig. 5.6) and lie in no preferred orientation within the bonebed. This is suggestive of valves that may have been exposed for long enough for the muscles that held the valves together to break down before being picked up and deposited with the other fossil material. The *Leperditia* is complete with an oxidized surface (Text-fig. 5.9), this completeness might point to a lack of transport and potentially that the *Leperditia* died where it had lived.

The taphonomy of the eurypterids also supports this allochthonous, high energy setting for the DBB. Although they are recorded in the DBB, the eurypterids are not found articulated, although it appears that some specimens from Weir Quarry may have been (Manning 1993). All of the eurypterid material seen in the DBB at Weir Quarry has been fragmented, with only the specimen figured in this chapter (Text-fig. 5.10) being identifiable. The organic cuticle was broken and fragmented before being deposited. As the eurypterids were likely some of the largest animals living in the Downton Sea, many of the taphonomic pathways described within Chapter 4 could also have been at work upon the carcass of a eurypterid. Unlike the fish though, having an organic carapace would make them more susceptible to destructive taphonomic processes over time unless quickly buried.

5.3 Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Order Modiomorphida Newell, 1969
Family Modiomorphidae Miller, 1877

Genus MODIOLOPSIS Hall, 1847

Type species: *Pterinea modiolaris* Conrad, 1838, U.S.A., from New York.

Modiolopsis complanata (Sowerby, in Murchison, 1839)
Text Figures 5.4 & 5.7

1839 *Pullastra complanata* Sowerby, in Murchison p. 609, pl. 5, fig. 7.
1859 *Modiolopsis complanata*; Sowerby, in Murchison, p. 645, pl. 23, fig. 1.
2013 *Modiolopsis complanata* Sowerby; Blieck, et al. p. 33

Type material: Geol.Soc.Coll. 6660 as described by Sowerby, in Murchison (1839), p. 609, pl. 5, fig. 7. It is unclear if this is regarded as the type specimen but it does represent the first described specimen.

Text figure 5.7 DBBM3, bedding surface with numerous *Modiolopsis complanata* as internal and external moulds. Scale is 6 cm.

Material: Ten specimens on DBBM3, with seven being measurable, preserved as internal and external moulds.

Diagnosis (modified from Sowerby 1839): Transversely elongated, twice as wide as long, smooth, rather flat; anterior extremity small, rounded; posterior extremity pointed, its edge oblique; beaks not prominent, very near the anterior extremity.

Description: Size ranges from 15-30 mm from anterior to posterior and measuring 8-14 mm from dorsal to ventral. Unfortunately, due to the small sample size, it is not possible to determine whether there is a bias on the presence of left or right valves. On valves which have a darker oxidised appearance growth lines can be seen. There are c. 18 growth lines c. <1mm apart.

Remarks: Further valves are almost certainly present in samples from the DBB at Weir Quarry but are seen only in cross-section.

Class Gastropoda Cuvier, 1795

Order Euomphalina De Koninck, 1881

Family Pycnomphalidae Peel, 1984

Genus TURBOCHEILUS Perner 1907

Turbocheilus helicites (Sowerby in Murchison, 1839)

Text Figures 5.5, 5.8

1839 *Trochus helicites*, J. de C. Sowerby, in Murchison p. 603, pl. 3 figs, 1e and 5.

1859 *Platyschisma helicites*; J. de C. Sowerby, in Murchison, p. 533, pl. 26, fig. 9. pl. 34, fig. 12.

1984 *Turbocheilus helicites*; Peel, p. 80.

Type Material: There is no referred type specimen, and therefore, a neotype should be established.

Material: There are only three specimens sufficiently well preserved (as internal and external moulds) for study within the material collected from Weir Quarry.

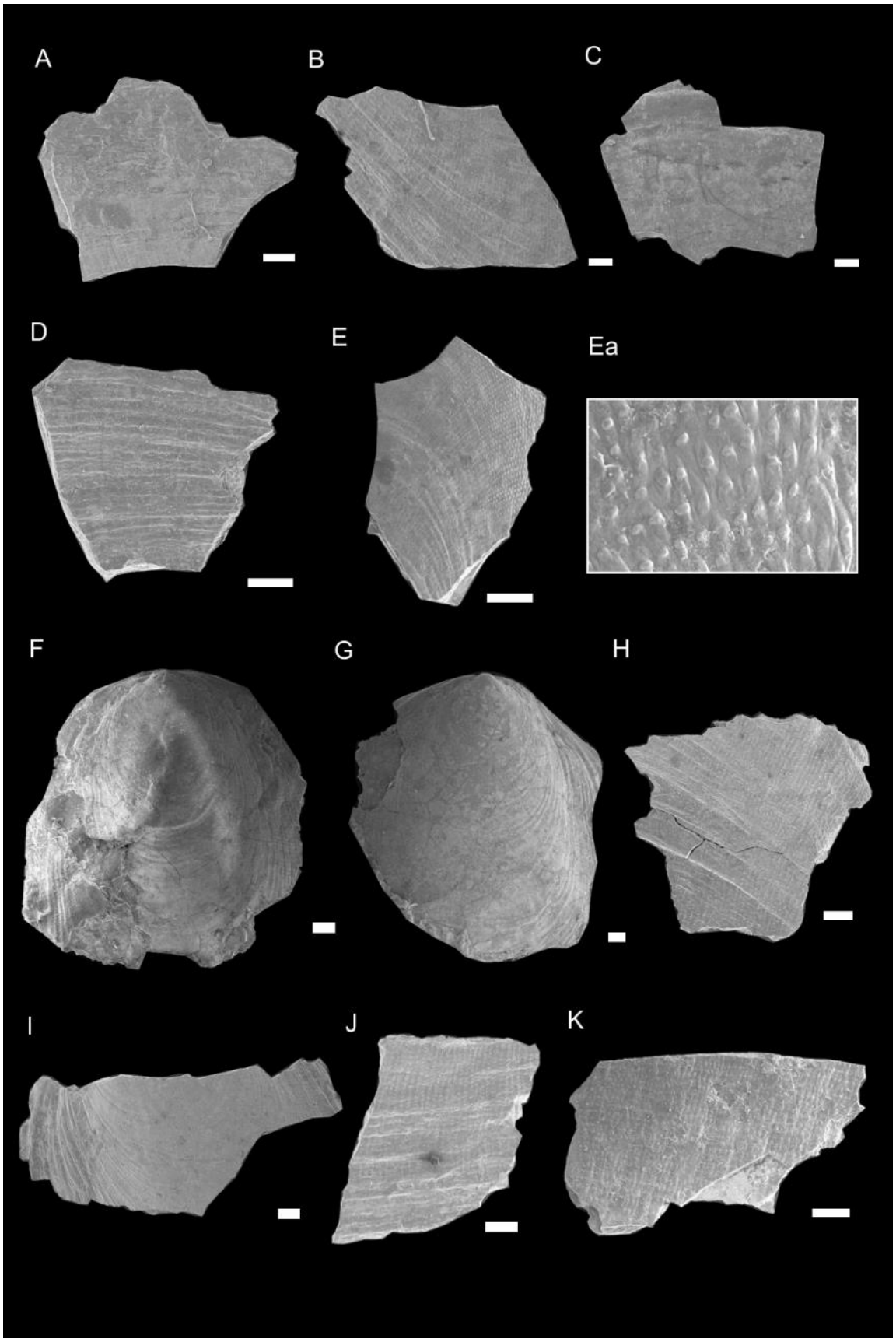
Diagnosis (modified from Sowerby 1839): Depressed, smooth, convex beneath; whorls about 4, hardly convex above (except in cast), obtusely angular at the margin of the base; umbilicus small and deep.

Description: Shell is laterally compressed and trochospirally coiled. The shell has a broad whorl. Shells are 14 mm wide and 4 mm high.

Remarks: No taxonomic work has been carried on this taxon since its first discovery. This is the reason that there is no designated type material.

Text figure 5.8 The two best-preserved specimens of *Turbocheilus helicites* DBBM5; scale bars represent 6 mm for the top image and 7 mm in the bottom image.

Plate 5.1



Explanation of Plate 5.1

Fig. A-D fragments of *Tunisiglossa cornea* Cocks and Popov; E, H-K fragments of *Lingula missendenensis* Straw with Ea a close-up of E showing ornamentation on the shell. F-G near complete valve of *Lingula missendenensis* Straw. A) DBB5.500 4 B) DBB20.500.2 C) DBB5.500.2 D) DBB5.212.3 E) S212.z2 Ea) S212.z2.a F) DBB19.500.2 G) DBB19.500.2 H) DBB20.500.4 I) DBB20.500.5 J) DBB20.500.1 K) DBB7.212.1. A-K in oblique lateral view. Scale bars represent 100 μm.

Class Lingulata Gorjansky and Popov, 1986

Order Lingulida Waagen, 1885

Family Obolidae King, 1846

Genus TUNISIGLOSSA Massa, Havlíček & Bonnefous, 1977

Type species: *Tunisiglossa tripolitanea* Massa, Havlíček, and Bonnefous, 1977, from Libya.

Tunisiglossa cornea Sowerby (in Murchison, 1839)

Plate 5.1, Figures A-D

1839 *Lingula cornea* J. de C. Sowerby, in Murchison, p. 603, pl. 3, fig. 3.

1839 *Lingula minima* J. de C. Sowerby, in Murchison, p. 612, pl. 5, fig. 23.

? 1866 *Lingula unguiculus*, (Salter MS); Davidson, p. 48, pl. 2, figs 42–44.

2009 *Tunisiglossa*? *cornea*; Cocks and Popov, p.362, pl. 2, fig. 19; pl. 3, fig. 11; figs 1B, 2A–L

Type specimens (after Cocks and Popov 2009): The lectotype of *cornea*, selected by Cocks, (1978, p. 8), GSM Geol. Soc. Coll. 6637, illustrated by Bassett (1986), the original of J. de C. Sowerby (1839), from Downtonian Beds, Tin Mill, Downton, Shropshire. The lectotype of *minima*, selected by Cocks, (1978, p. 9), GSM Geol. Soc. Coll. 6640, illustrated by Bassett (1986), the original of J. de C. Sowerby (1839), pl. 5, fig. 23) from beds of Ludfordian age, Delbury Common, Shropshire.

Material: Eleven fragments of shell were of significant quality and size to identify.

Diagnosis (after Cocks and Popov 2009): Shell subequally biconvex elongate, suboval, 160–179% as long as wide with maximum width slightly anterior to mid-length in adult specimens. Ventral valve gently convex, with a narrow triangular pseudointerarea bisected by a narrow pedicle groove with subparallel lateral sides and with flexure lines on slightly raised propareas. Dorsal valve gently convex with a thickened posterior margin lacking pseudointerarea. Ventral valve interior with elongated visceral area extending anteriorly up to two-thirds valve length, with weak

impressions of the outside lateral, middle lateral and central muscles at the anterior ends of elongate subtriangular muscle tracks. Ventral transmedian and anterior lateral muscle scars situated on the pair of oblique low ridges bounding the posterolateral margins of the visceral area: their individual scars seen only in adult specimens. Pair of umbonal muscles situated outside the pedicle nerve impression, represented by a pair of fine grooves becoming almost parallel in the anterior half of the visceral area. Ventral vascula lateralia submarginal but at some distance from the shell margins. Dorsal interior with a weakly-defined visceral area extending anteriorly to about 60% of valve length, with closely-placed, weakly-impressed central and anterior lateral muscle scars. Individual dorsal scars of transmedial, outside lateral and middle lateral muscles usually not seen except in gerontic specimens on the swollen posterolateral margins of the dorsal visceral area. Dorsal median septum usually absent. Dorsal vascula media fine, subparallel; vascula lateralia slightly converging anteriorly.

Description: The largest fragment has a height of 3 mm by a width of 2 mm, while the smallest is 0.5 mm by 0.42 mm.

Remarks: *T. cornea* can be distinguished from the other lingulate brachiopod in the DBB, *Lingula missendenensis*, primarily by its lack of ornamentation.

Family Lingulidae Gray, 1840

Genus LINGULA Bruguiére, 1797

Type Species: *Lingula missendenensis* Straw, 1933, from Little Missenden, Oxfordshire

Lingula missendenensis (Straw, 1933)

Plate 5.1, Figures E-K

1933 *Lingula missendenensis* Straw, p. 114, pl. 9, figs 3a, b.

1933 *Lingula zigzag* Straw, p. 115, pl. 9, figs 4a, b.

1978 *Lingula missendenensis* Straw; Cocks, p. 9.

1978 *Lingula zigzag* Straw; Cocks, p. 11.

Holotype: GSM 51859; that of *L. zigzag* which is a junior synonym of *L. missendenensis*, the holotype of which is, according to Cocks and Popov (2009), Geol. Survey Museum 51860A.

Material: 2 near complete valves (DBB19 500 1 and DBB19 500 2) and 13 fragments.

Description: DBB19 500 1 (Plate 6.2, fig. I) has an umbo to anterior margin measurement of 1.4 mm and a valve width of 1.2 mm. The valve has surface ornamentation: radiating ornamentation running the length of the valve. This is the most diagnostic feature used to distinguish this species from other brachiopod fragments in the residues. The shell is convex and sub-oval in shape.

Class Ostracoda Latreille, 1802

Order Beyrichicopida Pokorny, 1954

Family Beyrichiidae Jones, 1855

Genus FROSTIELLA Martinsson, 1963

Type Species: *Frostiella groenvalliana* Martinsson, 1963, from Ludlow, Shropshire.

Frostiella groenvalliana Martinsson, 1963

Plate 5.2, Figures A-C

1909 *Kloedenia wilckensiana* Jones et var. *plicata* Jones; Moberg and Grönwall, pl. 6, figs 6, 7.

1963 *Frostiella groenvalliana* n. sp., Martinsson, p. 5 figs 7C, 8, 14, 15A, 15B, 16A, 16B, 17A-F.

2016 *Frostiella groenvalliana* Martinsson; Hauser, p. 64, fig. 4 F.

Holotype: Held in the Palaeontological Institute, University of Lund, Sweden, No. 4084T, a left valve of a female. Paratypes are held in the Museum für Naturkunde Berlin, nos, MB.O. 174-177 and MB.O. 178 & 179 (figured in Martinsson 1963).

Material: Three valves preserved as internal moulds, with numerous valves present along bedding planes of the DBB bone bed horizon at Weir Quarry.

Diagnosis (after Martinsson 1963): Kloedeniinae with crumina strongly assimilated with the domicilum; crumina with a narrow, striate, and somewhat swollen field between the distinct velar blend and the marginal structure. Syllobium with protruding cusp.

Description: Due to the preservation, it is difficult to give a full description. However, a few details can be observed, such as a well-defined preadductorial lobe which is higher than the anterior lobe as well as the syllobium (cusp), with a shallow prenodal.

Remarks: Due to the dissolution of valves through diagenesis detail has been lost except for gross morphology.

Genus LONDINIA Martinsson, 1963

Type species: *Londinia arisaigensis* Copeland, 1964, from Arisaig, Nova Scotia.

Londinia arisaigensis Copeland, 1964
Plate 5.2, Figures C-F

1964 *Londinia arisaigensis* Copeland, p. 11, figs 16-26.
1995 *Londinia arisaigensis* Copeland; Miller, pl. 2, figs 13-14.
2013 *Londinia arisaigensis* Copeland; Perrier and Siveter p. 360, fig. 22.5.

Holotype: Held in the Canadian Geological Survey, Ottawa, No. GSC 14562. Figured by Copeland, 1964, pl.1, fig. 18, from the Stonehouse Formation (upper Silurian), Arisaig, Nova Scotia.

Material: 22 casts of external moulds and one external mould, with numerous valves along bedding planes.

Diagnosis (after Siveter in Whittaker and Hart 2009): *Londinia* with indistinctly asymmetrical lobal arrangement. Anterior syllobial lobule long, slender, sloping forwards; preadductorial node slightly broader, less elongate, both lobes strongly elevated above other parts of valve, with tendency to develop lateral facets on their dorsal crests. Anterior lobe joined, anteroventrally, to elevated lobal connection beneath adductorial sulcus; more prominent than rather isolated posterior syllobial lobule.

Description: Due to the preservation, it is difficult to give a full description. Specimens have a prominent preadductorial lobe; the syllobium cusp is well developed with a narrow prenodal between the preadductorial lobe and the anterior lobe, which is wider between the preadductorial lobe and the syllobium cusp. On one heteromorph an inflated brood pouch can be observed.

Remarks: Despite the low numbers of figured specimens, some surfaces are covered in ostracods. It is estimated that over a 25 cm^2 area there would be 330 ostracods, based on 33 ostracodes counted from a 2.5 cm field of view (under a light microscope).

Incertae sedis
Order Leperditicopida Scott, 1961
Family Leperditiidae Jones, 1856

Genus LEPERDITIA Rouault, 1851

Leperditia sp.
Text Figure 5.9

Species indeterminate

1995 *Leperditia* sp; Miller p. 356, pl. 2, fig. 18.

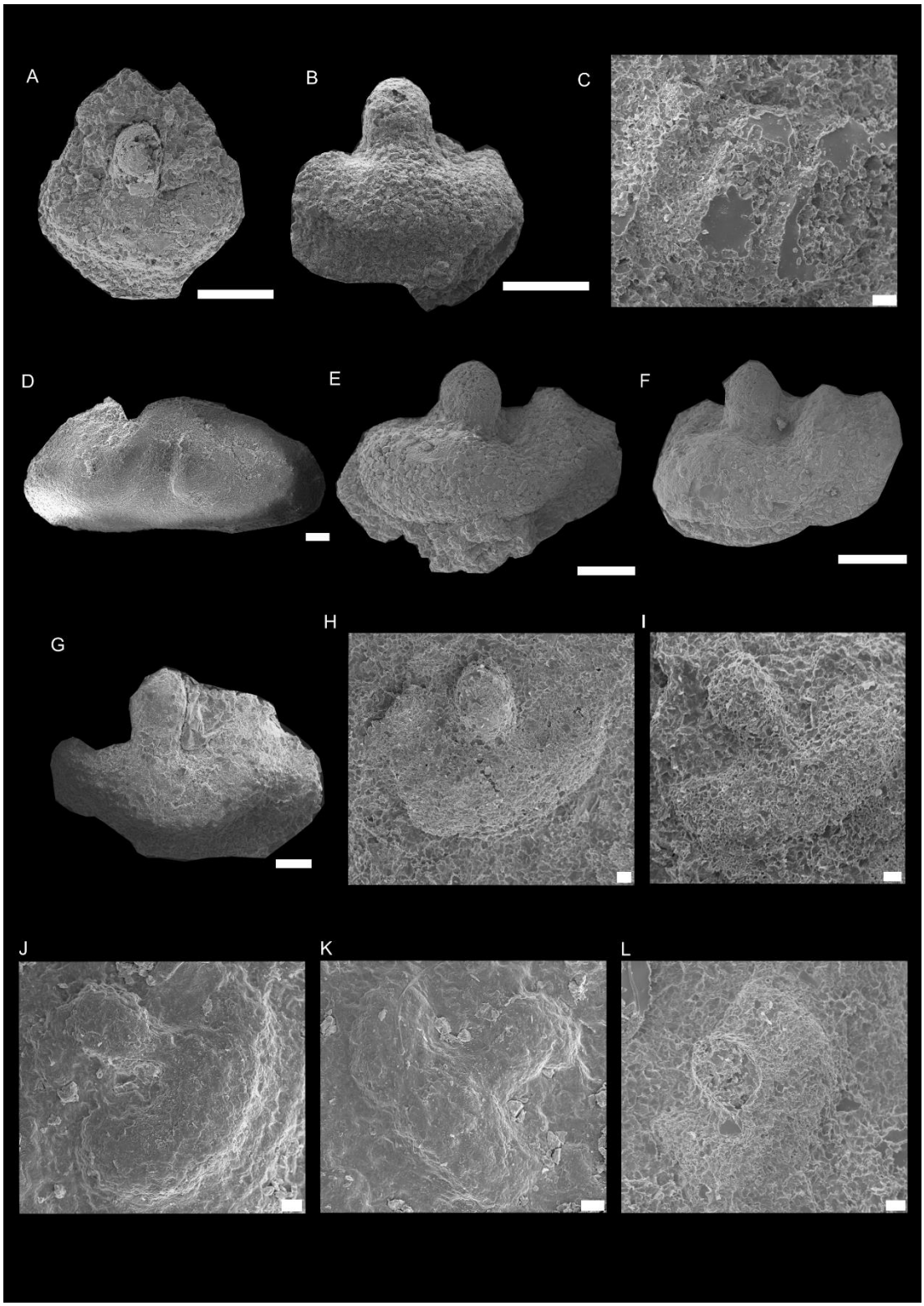
Material: 2 specimens DBBM9, preserved as internal mould, from the DBB at Weir quarry.

Description: Smooth valve, maximum 7 mm long and 5 mm wide (Text-fig. 5.9); hinge located on the dorsal side of the valve which is flat in appearance, while on the ventral side the valve is curved.

Remarks: *Leperditia* is an important taxon to help determine the palaeoenvironmental conditions (Siveter 1984), discussed in chapter 9.

Text figure 5.9 DBBM9 *Leperditia* sp. scale is 1 mm.

Plate 5.2



Explanation of Plate 5.2

Figs A-C *Frostiella groenvalliana* Martinsson A) tecnomorph DBB20B.500.1 B) tecnomorph DBB7.500.1 C) tecnomorph DBBM8 1. D Non-palaeocope D) DBB18.500.1. E-L *Londinia arisaigensis* Copeland E) heteromorph DBB18.500.3. F) tecnomorph DBB18.500.2. G) tecnomorph DBB14.5.500.1. H) tecnomorph DBBM8 2. I) tecnomorph DBB8M 3. J) tecnomorph DBB8M 4. K) tecnomorph DBB8M 5. L) tecnomorph DBBM8 6. A-D, G-L lateral view. E-F oblique lateral view. Scale bar represents 100 µm. A-B, D-G internal casts from Paraffin expansion method, C, H-I and L external casts using Coltene 4823, Type 2, medium consistency Polyvinylsiloxane J-K Milliput® Superfine white.

Incerti ordinis

Incertae familiae

Non-palaeocope

Plate 5.2, Figure D

Material: 2 specimens, one preserved as an internal mould and one as an external mould with sediment infill.

Description: DBB18 500 1 has a length of 0.85 mm and a height of 0.35 mm (Plate 5.2, fig. D). There are no distinguishing features present to describe.

Class Merostomata Woodward, 1866

Order Eurypterida Burmeister, 1843

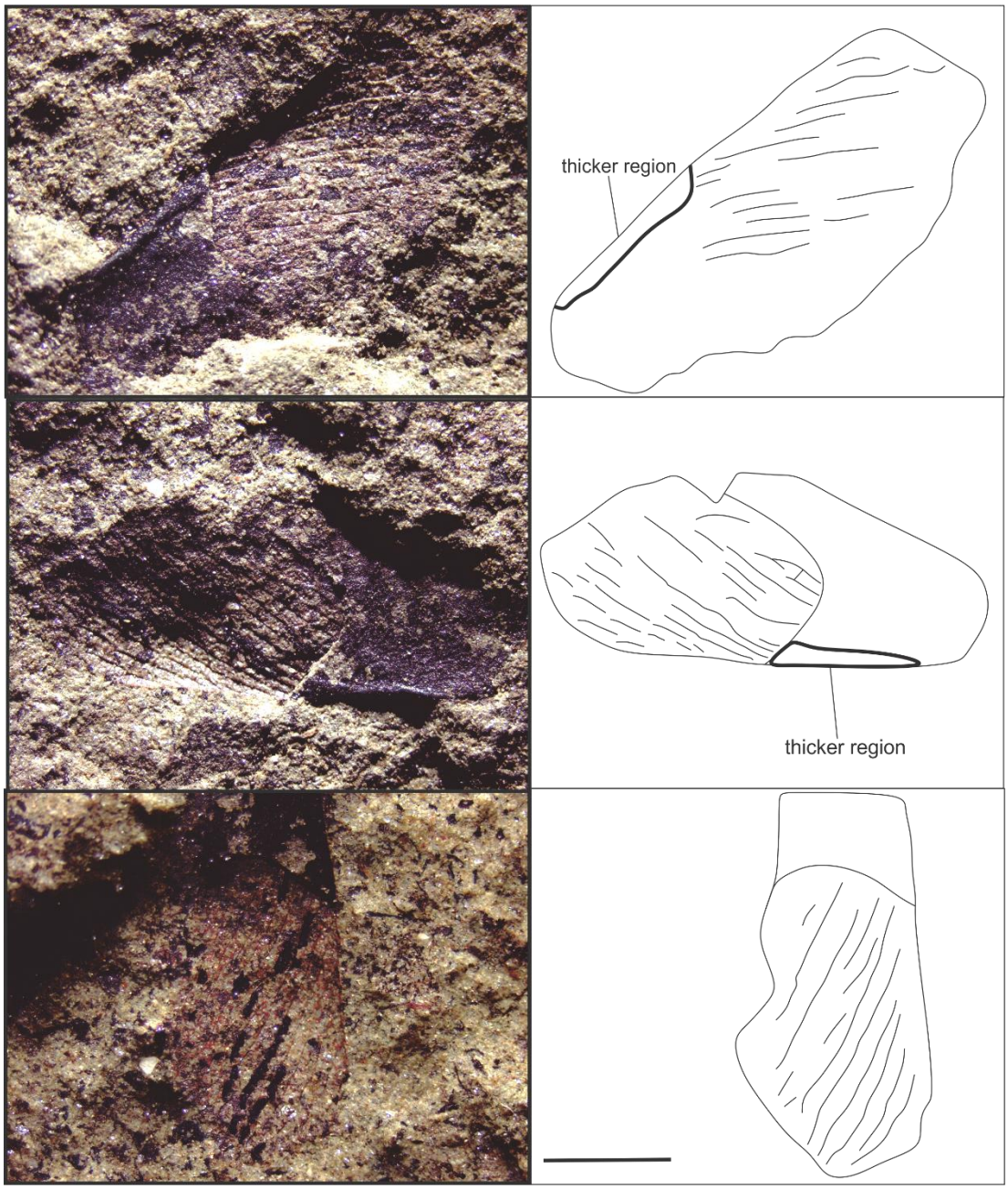
Incertae familiae

Genus and species indeterminate
Text Figure 5.10

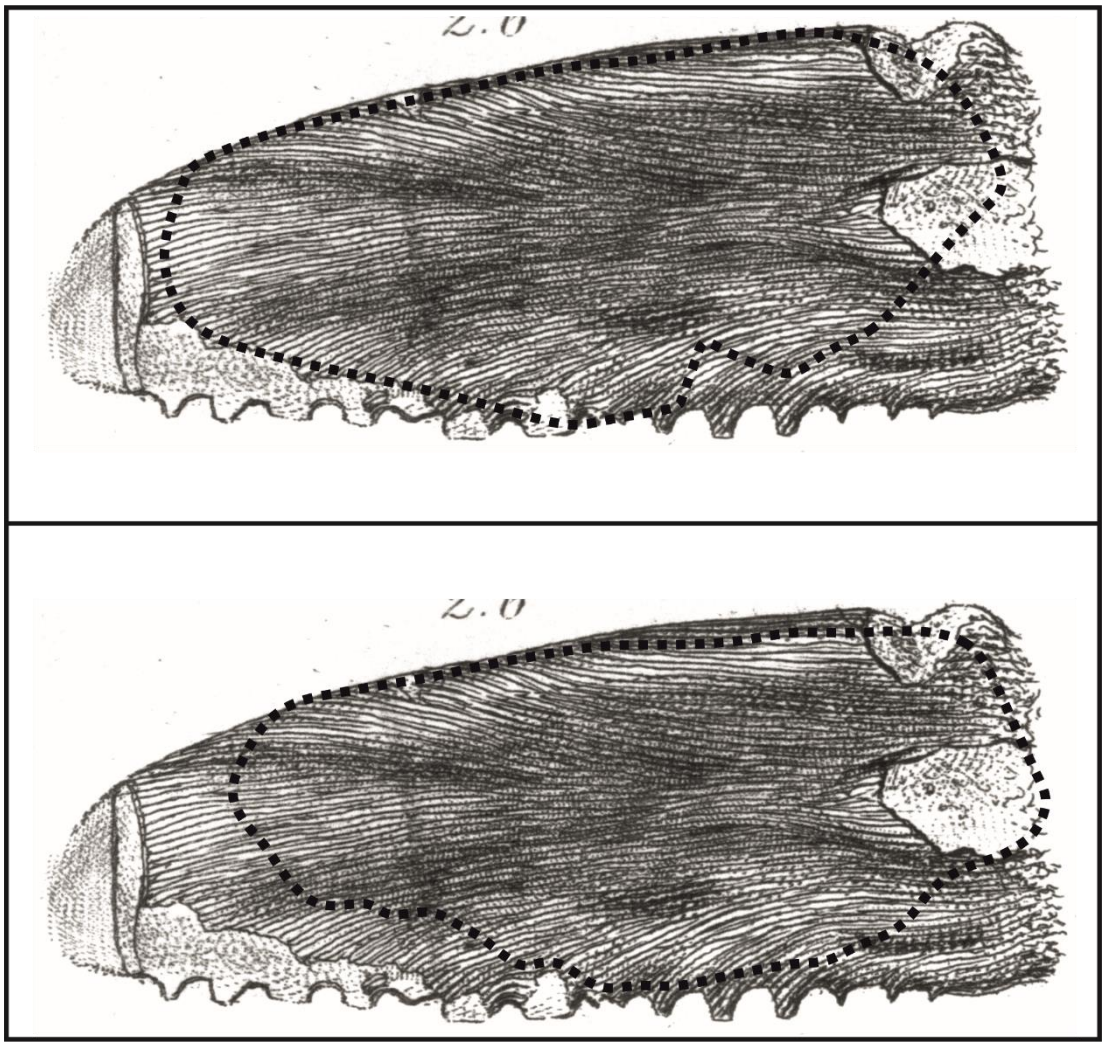
Material: 1 fragment found on a slab and counter slab DBBM 6 & 7, preserved as a black carbonised layer; numerous minute fragments on some of the organic-rich bedding surfaces.

Description: Fragment has a lobe-like form. Its length on DBBM 6 is 13.6 mm with a width of 6.3 mm at its widest point, while DBBM 7 has a length of 12.6 mm and width of 5.6 mm at its widest point. The surface is covered with structures that resemble venation running across its surface at a 45º angle (Text-fig. 5.10).

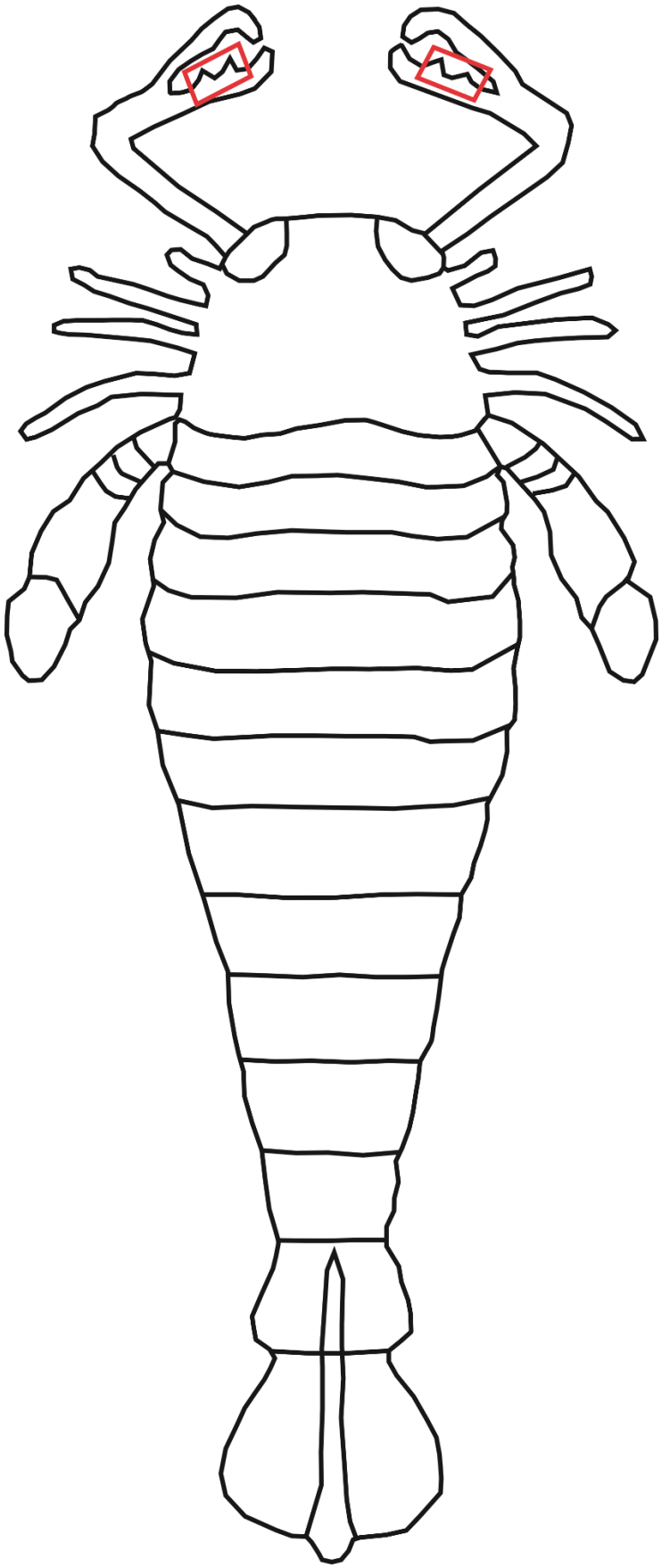
Remarks: Similarities with an illustration produced by Salter (1852, pl. 21, fig. 2b) of the chelicera of *Pterygotus problematicus* (Agassiz, 1839) (Text-fig. 5.11 and 5.12) are seen. This taxon became a nomen vanum and was replaced as *Erettopterus megalodon* (Kjellesvig-Waering, 1961). Later work by Tetlie (2006) provides a list of potential eurypterid taxa from the DCSF: *Erettopterus brodiei*, *E. spatulatus*, *Eurypterus cephalaspis*, *Nanahughmilleria pygmaea*, *Parahughmilleria salteri*, *Salteropterus abbreviatus*, *Slimonia* (?) *stylops*, *Marsupipterus sculpturatus* and *Hughmilleria banksii*.



Text figure 5.10 Possible eurypterid chelicera; DBBM 7 images taken in different orientations, and with light at differing oblique angles showing different details. The scale is 3 mm.



Text figure 5.11 Salter's (1852) illustration of a denticle from the chelicera of *Pterygotus problematicus* (Agassiz, 1839), now *Erettopterus megalodon* (Kjellesvig-Waering, 1961); the dotted line represents the outline of DBBM 6 and 7; a scale was not provided by Salter (1852).



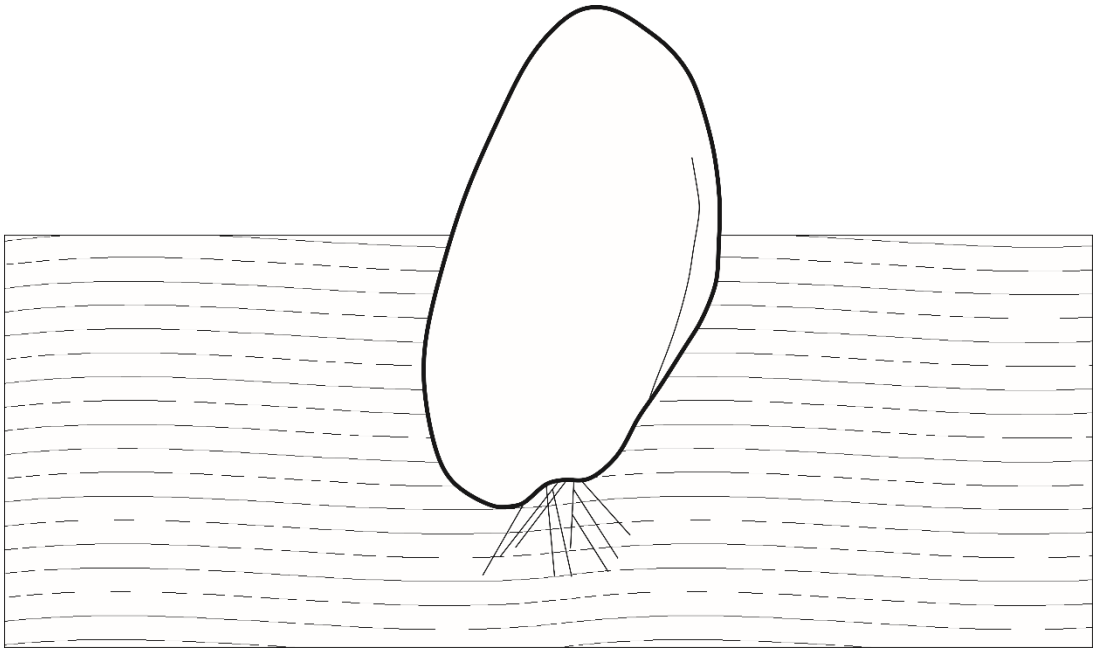
Text figure 5.12 Reconstruction of eurypterid, red boxes highlight areas from which the denticle would be present on the living animal.

5.4 Discussion

The invertebrates of the DBB are, like the vertebrates, not diverse, despite five classes being present. Within each of those classes, there are as few as one and at most 3 representatives. This points to a restricted setting that is limiting diversity.

5.4.1 Palaeoecology

Bivalves have a range of modes of life that can be determined by looking at the morphology of the shell (Stanley 1970). The interpreted paleoecology of the genus *Modiolopsis* is as a stationary semi-infaunal suspension feeder. This could mean that *Modiolopsis*, with its morphological similarities to modern mussels which are byssally attached, was endobyssate (Antia 1979; Kříž 1984). Certainly, this could explain how this bivalve was able to maintain its position on the seafloor by using byssal fibres to attach to the sediment (Text-fig. 5.13). Modern byssally attached bivalves also live gregariously. Despite this, there is no strong evidence that *Modiolopsis* were gregarious, although in the DBB and Platyschisma Shale elsewhere *Modiolopsis* are preserved together. This might suggest them having been picked up close to each other before being dumped rapidly or that, over time, shells were scattered on the sea bed.



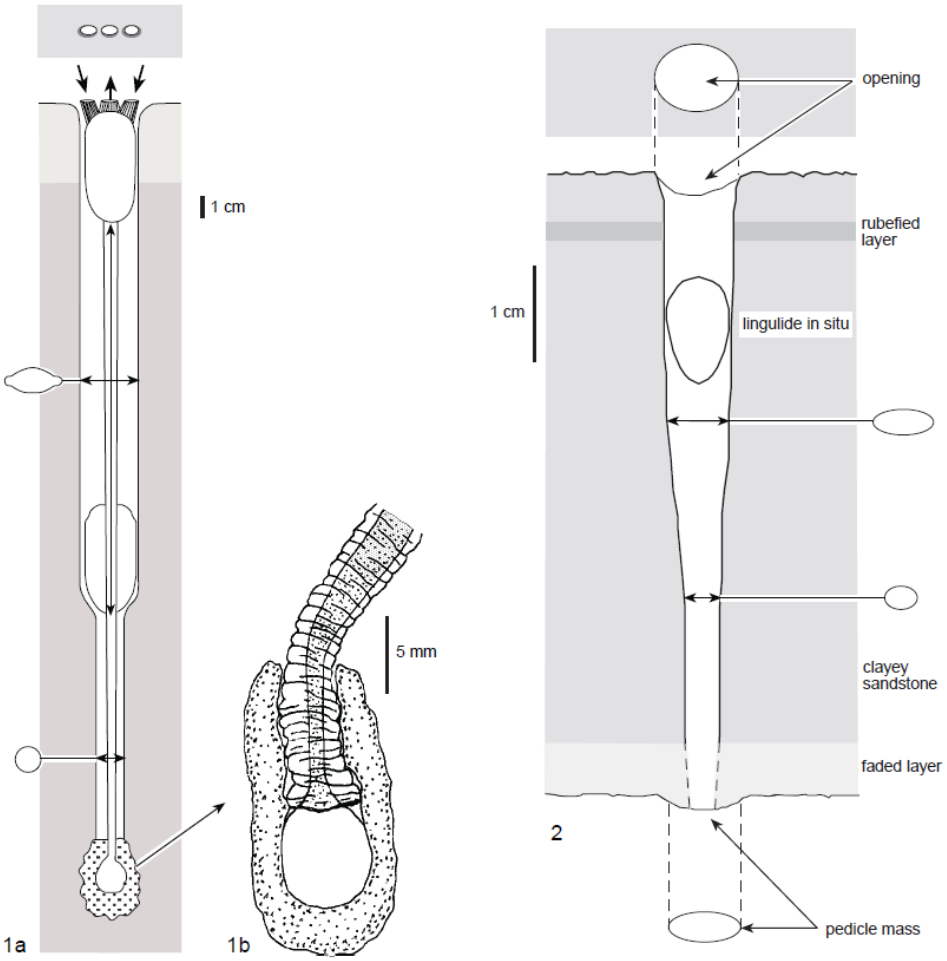
Text figure 5.13 Reconstruction of possible life habit of *Modiolopsis complanata.*

The inferred paleoecology of *Turbocheilus helicites* comes from Peel (1984) who suggested that it has morphological similarities to the lenticular pleurotomariin *Liospira*. *Liospira* has a near radial aperture, which is suggestive of a relatively immobile existence with its shell lying flat on the substratum. The genus is represented in both soft-bottom sediments and shallow-water sandy sediments in the Silurian of Arisaig. Peel (1984) suggested that *T. helicites* also has the same association with shallow water, but there are differences noted between the two taxa: *Turbocheilus helicites* has instead of the peripheral sinus a sub-sutural sinus. This suggests a single gill rather than the two of *Liospira* (Peel 1984). There is also a suggested modern analogue for *T. helicites*, which is the living trochid *Umbonium vestiarium* (Peel 1984) found in large numbers in the Indian Ocean (Text-fig. 5.14). This snail lives in the eulittoral zone (foreshore) and its life habits and environment would be a good model for explaining why, historically, large slabs of PSM have been found with *T. helicites* covering them. It is suggested by Peel (1984) that due to morphological similarities between *T. helicites* and *U. vestiarium* that their mode of life may have been analogous .

Text figure 5.14 living trochid, the Button Snail (*Umbonium vestiarium*) in life position. (https://www.flickr.com/photos/wildsingapore/6111016226/in/photostream/).

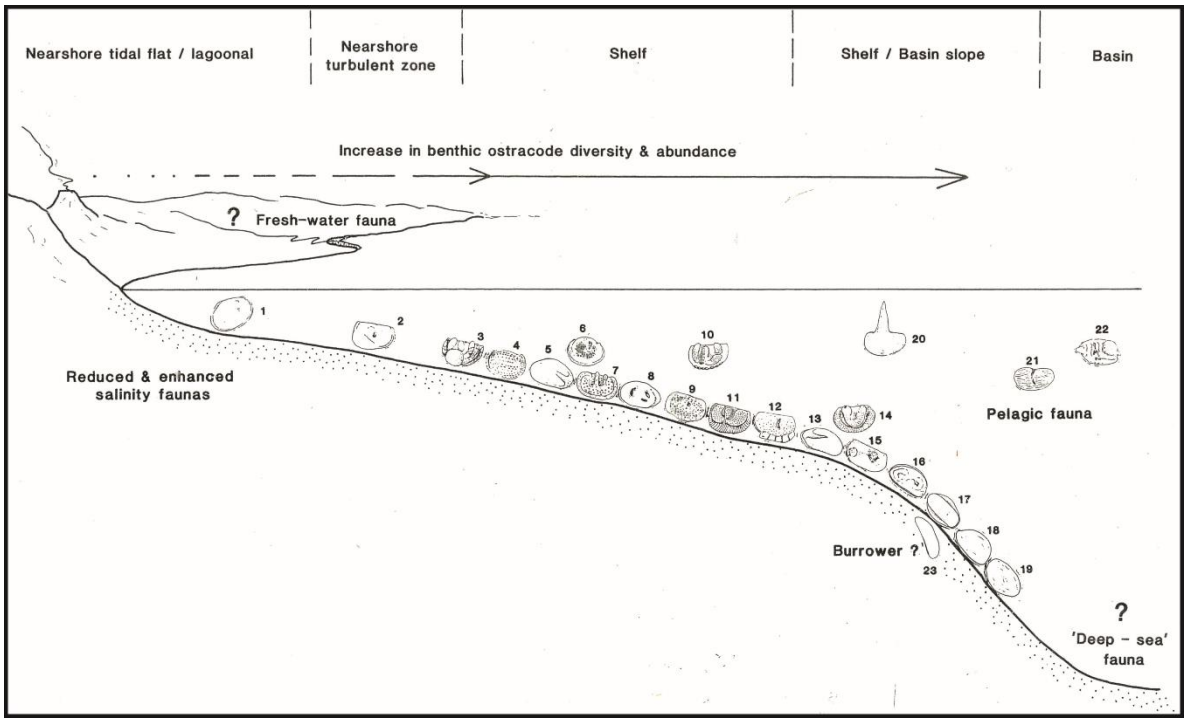
U. vestiarium feeds by filtering the pallial stream of water as it moves across the surface of the sand but can also be buried except for its tentacles, eyestalks and siphons. It will remain stationary or creep when buried (Fretter 1975). An important habit of *U. vestiarium* is that it will feed only when conditions are quiet. As discussed in the sedimentology chapter, the DBB was deposited in one of two energy conditions: rapid high energy and quiet lower energy. Bradfield (1999) named a community for *T. helicites*, including such taxa as *Modiolopsis*, *Frostiella groenvalliana*, *Leperditia* sp. and thelodonts. The community represented a restricted environment, probably lagoonal within a low salinity setting.

Both brachiopods present are from the class Lingulata. Today lingulates live exclusively in brackish to intertidal environments (Cherns 1979); however, considerable caution should be taken when using the environmental habits of modern *Lingula* to interpret fossil examples of the class as some fossil Lingulata have been found to have thrived in shelf and basinal regions (Cherns 1979). Cocks and Popov (2009) also discussed lingulid palaeoecology. They determined that, although there is common assumption that all "linguloids" lived in shallow water due in part to the linguloid communities established by Ziegler et al. (1968), which were interpreted as a nearshore environment in the Llandovery of the Welsh Borderlands, in the Silurian of the U.K. the ecology for the linguloids ranges from nearshore to deep shelf. Like the bivalves, though, it seems likely that the brachiopods were transported to the DBB due to them being represented by a large number of fragments and only small complete specimens. If compared to modern-day lingulids, such as *Lingula anatina* (Lamarck, 1801) which burrows in soft sediments, this would fit with the known palaeoenvironments. The shell of *L. anatina* is, however, more elongate and caution should be taken when making comparisons of fossil taxa with modern examples as mentioned previously. Despite this, one model for a life habit of *T. cornea* and *L. missendenensis* may have been as an infaunal burrower into soft sediment (Text-fig. 5.15).



Text figure 5.15 Longitudinal section of a burrow of a living lingulide with the shell in normal position and retracted (and *1b*, detailed pedicle mass); and *2*, of a fossil lingulide (Triassic of Vosges Mountains) (taken from Emig 1997).

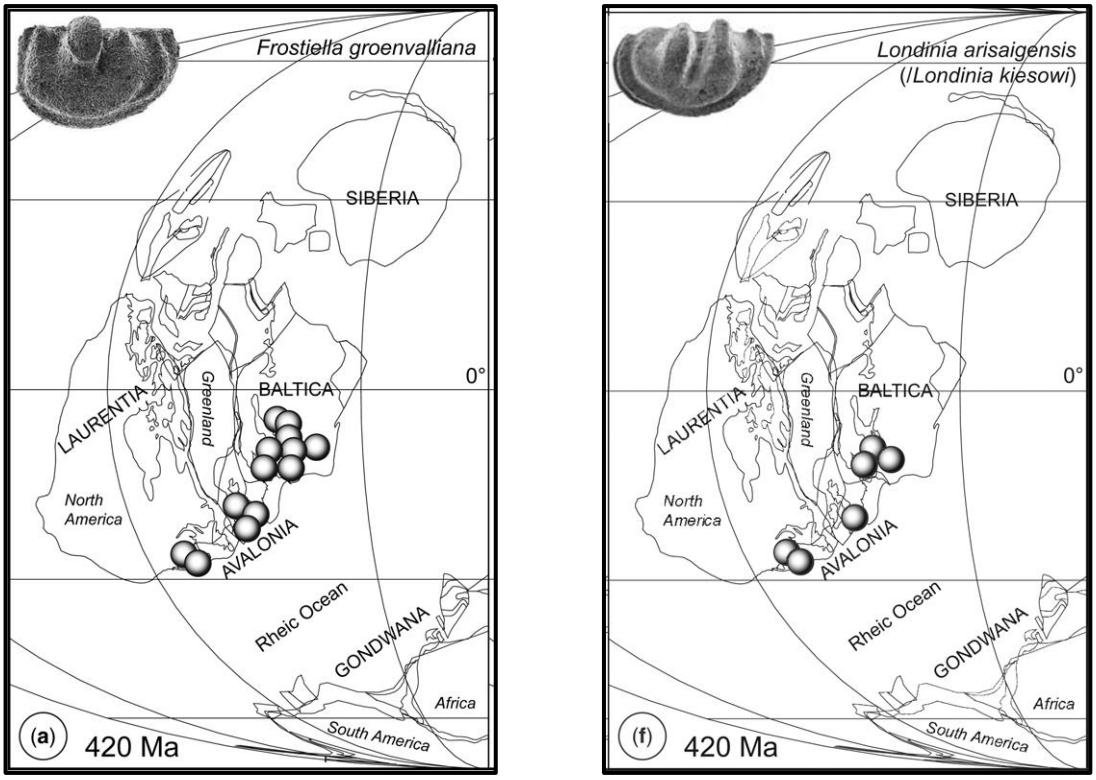
Ostracods are one of the best invertebrate groups to use as environmental indicators. Some genera have very restricted ecological ranges, for example, being found only close to shore or out in open water (Siveter 1984). There are three ostracods present in the DBB at Weir Quarry. The most common is *Londinia arisaigensis,* followed by *Frostiella groenvalliana,* which is interpreted as living in the shelf region (Text-fig. 5.14) (Siveter 1984; Miller 1995). The presence of *Leperditia* sp. provides more specific information on the environment. Leperditiids are known only from nearshore environments, as benthic swimmers or crawlers (Siveter 1984) although their assignment to Ostracoda is unclear (Tanaka et al. 2019); they may belong to another group of bivalved arthropods.



Text figure 5.16 Siveter's (1984) text-fig. 3 with placement of Silurian ostracods in their living environment. Of note for the DBB are the benthic crawlers and swimmers associated with nearshore tidal flats/lagoons (1); and the benthic crawlers and swimmers in near-shore, higher energy environments (1 & 2); and finally benthic crawlers and swimmers, open shelf to shelf slope (3, 10 & 11).

Miller (1995) recorded that the Platyschisma Shale Member has a sparse ostracod fauna with a maximum frequency of 0.2 ostracods per cm^2, and that only three beds yielded more than ten ostracods and that these had the same assemblages: *Frostiella*, *Londinia* and non-palaeocope ostracods. He noted that *Frostiella groenvalliana* is dominant; however, this is not the case in the DBB at Weir Quarry, where *Londinia arisaigensis* is most common. Siveter (1984) said that by the end of the Silurian, ostracods were occupying most marine environments and had taken up the majority of lifestyles known from modern ostracods. He continued, using evidence gathered from North America and other parts of Europe, stating that within the marine to restricted marine transition of the British Downton Group, ostracods for the first time had begun adapting to changes in salinity including reduced salinity, brackish water, and hypersaline conditions. Miller (1995) observed that both *F. groenvalliana* and *L. arisaigensis* appear to have been tolerant of a wide range of ecological settings. Ostracods also have a palaeogeographical application; their palaeogeography was recently discussed by Perrier and Siveter (2013) who summarised the distribution of

many taxa of Silurian ostracods, in particular, focusing on the late Silurian. The distribution of the two taxa seen in the DBB is mapped in Text-fig. 5.17. What is striking about the maps is that they show the same distribution as the vertebrates, suggesting that there was a continuity of palaeoenvironmental regime across Avalonia and Baltica during the late Silurian. It is important to note, however, that Perrier and Siveter (2013) still refer to the DCSF as being within the Přídolí Epoch. The work of Loydell and Frýda (2011) showed that the DCSF should be referred to the mid Ludfordian (Ludlow Epoch).



Text figure 5.17 Maps of ostracod distribution during the mid Ludfordian (taken form Perrier and Siveter 2013).

The eurypterids were, during the Silurian, most likely one of the top predators in their environments (Selden 1984). Indeed, they are the most likely taxa preserved in the DBB to have filled this ecological niche. Deducing palaeoenvironmental conditions from the limited eurypterid material in the DBB cannot be done due to the small data set and especially the ability for these organisms to be dispersed across the environments post mortem. However, the presence of eurypterid material does suggest that the DBB is at least from or near the environment where the eurypterid was living. Kjellesvig-Waering (1961) suggested that eurypterid palaeoecology could

be broken down into 3 “phases” the one of relevance to the DBB being the ‘Hughmilleriidae-Stylonuridae phase’ which Kjellesvig-Waering (1961) referred to being associated with clastic sediments and representing brackish bays and estuaries. Selden (1984) repeated this, citing the “Downton” of the Welsh Borderlands as being one of the type localities. Boucot (1975) updated the “phases” to reflect modern nomenclature. The Hughmilleriidae-Derpanopteridae-Stylonuridae assemblage he regarded as representing brackish to freshwater environments (Selden 1984).

6. Palaeobotany and Palynology

6.1 Introduction

This chapter focuses on the plants and organic-walled microfossils of the DBB at Weir Quarry. The chapter will describe previous work that is of relevance to this study. Comment will be made on the preservation of the plants and organic walled material. Descriptions of all of the plants and organic walled material found in the DBB at Weir Quarry are provided, in the style of the journal *Palaeontology*. Finally, there will be a discussion on the findings of this chapter.

6.1.1 Previous work

The study of Siluro-Devonian palaeobotany in the Welsh borders has been ongoing since Murchison (1839) first referred to plant material being found. Phillips (1848), who had worked at Perton Quarry, found one of the first plant-like fossils, which were rounded masses that Murchison had described as being animal in origin. This identification was found to be incorrect (Strickland 1852), and it was named *Pachytheca sphaerica* by Strickland and Hooker (1853) who thought it to be a seed. Dawson (1859) described *Prototaxites*, later to be recorded from the Welsh borders, from the Devonian of Canada.

Dixon (1921), in his memoir on the rocks of Pembrokeshire produced one of the first multi-locality papers that featured plants, while Stamp (1923) also discussed plants as part of a more extensive geological study of the base of the Devonian paying particular attention to the Welsh Borders. However, it was Lang's (1937) paper 'On the plant remains from the Downtonian of England and Wales' that provided the first guide to the palaeobotany of the "Downtonian" (which includes the DCSF) which is of most interest to this study. He described many of the plants and plant-like fossils found in the DBB, such as *Cooksonia*, *P. sphaerica*, *Prototaxites* and *Nematothallus*. Work continued, mostly focusing on the taxa from the upper Silurian and lower Devonian (e.g. Heard 1939).

A palynological study of particular note is that by Richardson and Lister (1969), who collected many samples at Downton Gorge including material from the LBB and

from the track that runs close to the DBB at Weir quarry. Their samples contained spores, and many other organic-walled microfossils and they identified several taxa, including *Synorisporites.* In the basal "Downtonian" at Ludlow and Gorsely (near Ross on Wye, Herefordshire), they noted that the spore assemblage was mostly the same as that from Weir Quarry. This paper was written when the term 'Downtonian' was still in use to describe the DCSF and the Temeside Shale Formation which were regarded as of Early Devonian age.

Edwards et al. (1995) described the ultrastructure of the spores of *Cooksonia pertoni*, with one of their principal localities being Ludford Corner. This work is important because it provides images and descriptions of material from the same member as the DBB material at Weir Quarry. In a similar study, Edwards et al. (1996) studied the ultrastructure of *Synorisporites downtonensis* and *Retusotriletes* cf. *coronadus* in spore masses from the Přídolí of the Welsh Borderland and discuss in detail these taxa. One of the two localities studied is again Ludford Corner the other was Weir Quarry making this one of the few papers that has looked at this latter locality.

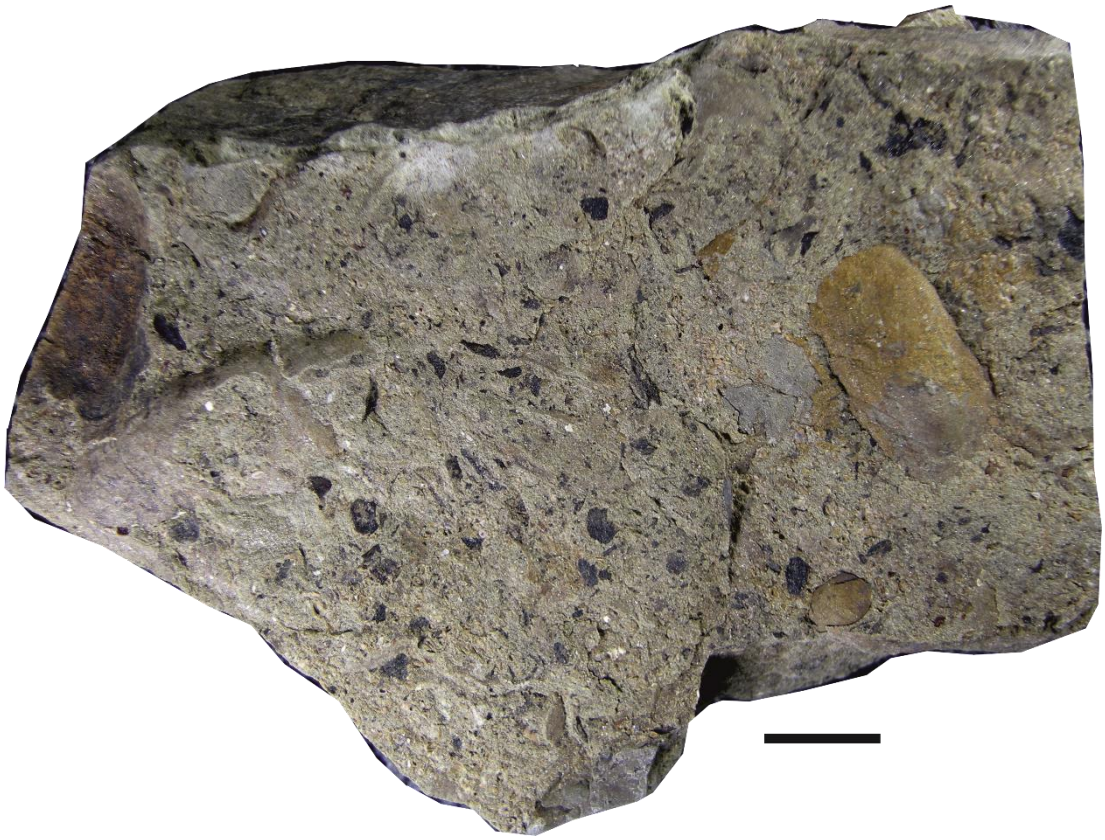
Glasspool et al. (2004) discussed the evidence for low-temperature wildfires, such as the black and silky lustre appearance of the cuticle and evidence seen under the SEM such as shrinkage resulting in distinctive ridges on the surface and blistering on the surface of the cuticle. This was found on some of the material found in the PSM of Ludford Corner.

The only in-depth study carried out at Weir Quarry on the palynology is that by Richardson and Rasul (1990). In this study, they collected 164 samples across the Welsh Borders, looking at the shelf and basinal areas. As this paper focuses on Weir Quarry, it will be discussed in detail in the discussion section (6.4) of this thesis.

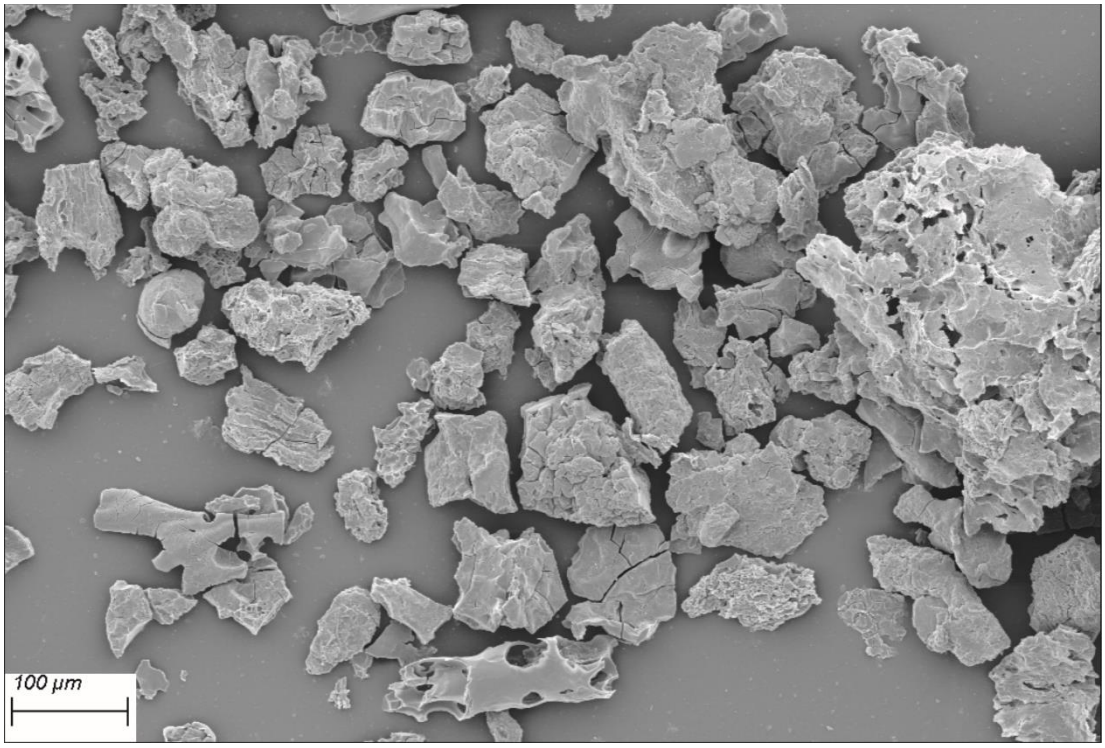
6.2 Preservation and taphonomy

6.2.1 Preservation

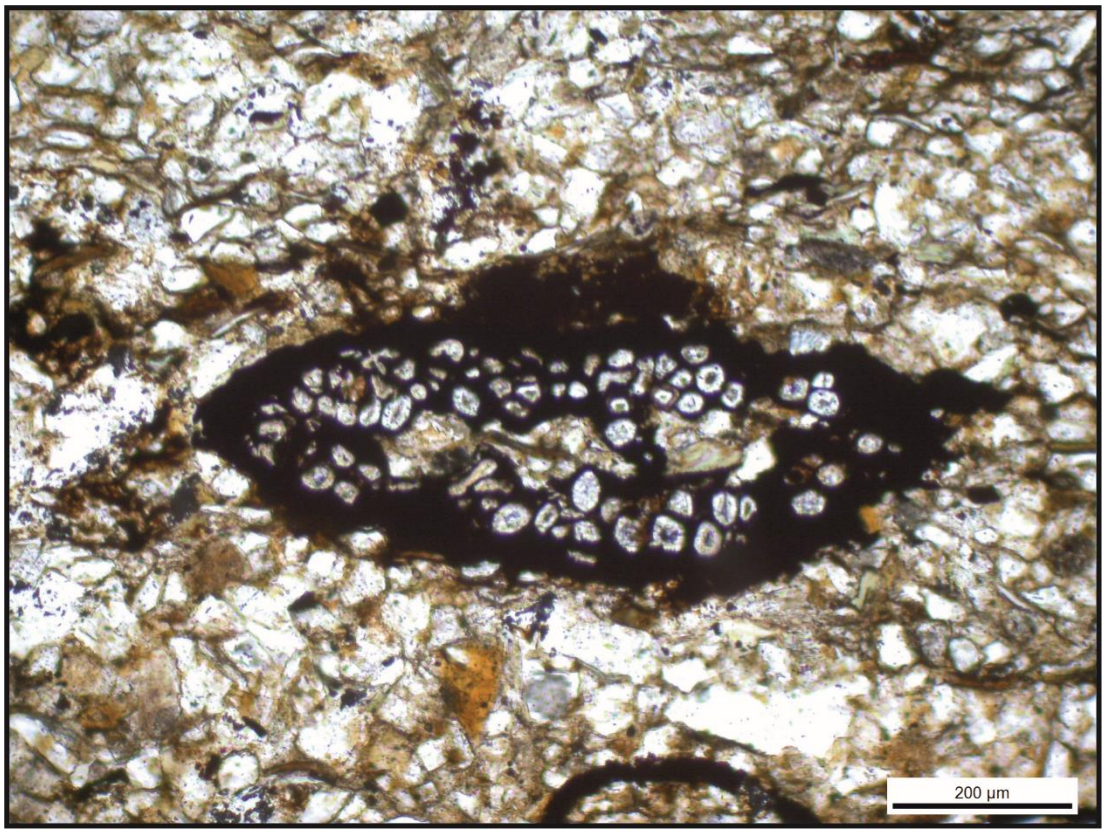
The plants and other organic-walled fossils are preserved as black carbonised fragments ≤2 cm in size. When examined in situ on the mica-rich bedding planes the appearance of the organic fossils could be described as "choppy" (Text-fig. 6.1 and 6.2), i.e. many of the fragments have very regular breaks like you would expect to see from the cut blades of grass after it has been mown. When studied on an SEM, many of the specimens can be seen to be compressed; others, however, have been preserved in 3D and seem to have resisted compaction. This can be seen in thin sections where the plant has resisted compaction so that even the relatively fragile "vascular" tissues have been preserved (Text-fig. 6.3). A possible reason for this extraordinary level of preservation was discussed by Glasspool et al. (2004) who looked at material from Ludford Lane, Shropshire. They found that low-temperature charring had occurred, as a result of "wildfires". Charcoalification is a process well known to lead to exceptional preservation in plants (Scott 2000); it altered the chemical and physical structure of the fossils, making them resistant not only to compaction but also to decay.



Text figure 6.1 Example of "choppy" appearance of the organic-walled/plant material on bedding planes within the DBB. The scale represents 1cm.



Text figure 6.2 Example of "choppy" appearance of the paly/plant material from HF residues within the DBB



Text figure 6.3 Cross-section of plant material from the DBBI1 showing evidence of 3D preservation due to charcoalification, with possible vascular cavities remaining open.

6.2.2 Taphonomy

As mentioned above, many of the plants appear to have been burnt in low-temperature (<400°C) wildfires (Glasspool et al. 2004). However, this does not explain how the plants entered the sediments at Weir Quarry. This is especially important as all of the plants found in the DBB at Weir Quarry are terrestrial. This, of course, has an impact on the palaeoecological model which will be covered in the discussion.

There are two main ways by which the plant material may have ended up within the bone bed; either the material was washed out from a fluvial terrestrial setting, or it may have been windblown into a marine environment. The plants and walled organic fossil are like most of the fossils found in the DBB at Weir Quarry in that they show both near-complete and fragmented material. It is, of course, unclear why some material is fragmented to the point that identification is not possible, while others are preserved with great detail present. A possible model is as discussed in previous chapters that there are two events taking place, with the more fragmented material

having spent more time in the environment, allowing it to become more fragmented before finally being buried, while the better, more complete material appears to have spent less time exposed to the environment before it was deposited. So far, there have been multiple lines of evidence to suggest that a high energy event was responsible for the deposition of the DBB at Weir Quarry. However, as mentioned in Glasspool et al. (2004), the plants and fungi were most likely desiccated before being burnt; modern plants which become desiccated are often delicate and are prone to breakage. Thus, little energy would have been required to break or fragment material and this may have occurred during transport itself.

6.3 Systematic palaeontology

Class Eutracheophytes Kenrick and Crane, 1997

Order Incerti ordinis

Family Incertae familiae

Genus COOKSONIA Lang, 1937

Type species: *Cooksonia pertoni* Lang, 1937; from Perton Quarry, Herefordshire.

Cooksonia pertoni Lang, 1937

Plate 6.1, Figures A-J; Plate 6.2, Figures A-G

1937 *Cooksonia pertoni* Lang, p. 7, pl. 8, figs 4-19, pl. 9, figs 20-27.
1992 *Cooksonia pertoni*; Edwards et al., l pp. 683-685, fig. 1.
1995 *Cooksonia pertoni*; Edwards et al., pp. 153-167, pl. 1
figs 1-8, pl. 2 figs 3-7.
1997 *Cooksonia pertoni*; Kendrick and Crane, pp. 34-35, fig. 3.
2004 *Cooksonia pertoni*; Edwards and Richardson, pp. 375, 377, 394, pls 3-4.
2008 *Cooksonia pertoni*; Gensel, p. 468, fig. 3.

Lectotype (established by Gonez and Gerrienne 2010): Lang no. 1242/V58011 (Lang 1937, pl. VIII, fig. 8). This is the first specimen illustrated by Lang and the best preserved in the original material collection housed in the NHM.

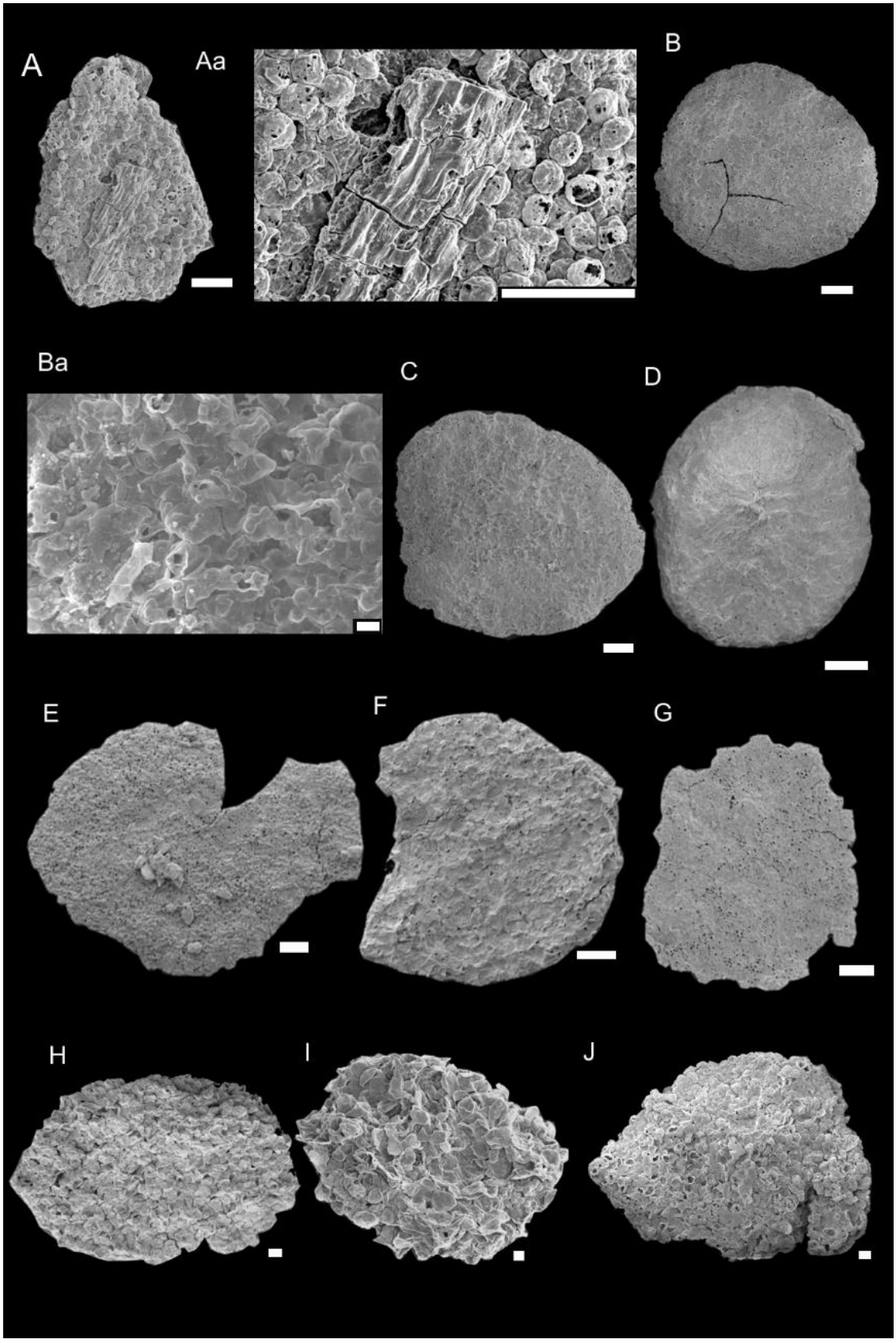
Material: 44 specimens recovered from processing using both the paraffin expansion method (Hauser 2016) and HCL-HF-HCL from the DBB at Weir Quarry: 28 are sporangia, 16 are axes.

Description: Sporangia are preserved mostly as compressed circular to ovate disks; there are a few specimens that are preserved in 3D (Plate 6.1, fig. A). Some of the sporangia are naked, lacking any spores (Plate 6.1, fig. D). The sporangia that do have spores present on the compressed specimens show flattened and folded spores often having a blister-like sculpture on their surfaces. The 3D specimens (Plate 6.1, fig. A) show the spores in their spherical form but with the same blistered ornamentation. Many of the spores appear damaged; it is uncertain what the cause of this damage is. The approximate average width of the sporangia is ≤760 µm. Axes are also preserved in two modes: compressed and 3D. They show parallel lines running along their length; none of the axes shows any evidence of pores. The fragmentary specimens all have sharp breaks, while the 3D specimens have smoother, more rounded breaks. The axes also show evidence of bifurcation (Plate 6.2, fig. G).

Remarks: No trilete mark is seen on any of the spores; however, as is mentioned in Edwards et al. (1995) superficial sutures are rarely seen in SEM; in fact, they used TEM (Transmitting Light Microscope) in the paper. Due to the fragmentary nature of *Cooksonia* fossils, it has been suggested (Taylor et al. 2009) that all of the *Cooksonia* specimens described to date may represent the distal branches of a much larger plant, but the uniform size of many specimens described points to the interpretation of *Cooksonia* as a small plant. *Cooksonia* is considered to represent one of the oldest vascular plants; however, when Lang (1937) originally described the genus none of the specimens with terminal sporangia had preserved conducting elements; the presence of a central strand composed of specialised (perhaps conducting) cells was observed only in isolated axes lacking sporangia (Taylor et al. 2009). *Cooksonia* has conducting elements that are different from those of true vascular plants and which may have had a different evolutionary origin (Taylor et al. 2009). In addition to axes lacking clearly defined vascular tissue, specimens of *Cooksonia* have been reported with a variety of sporangial morphologies (Gonez and Gerrienne 2010), variously ornamented spores, axes with and without stomata, and various forms of branching. Due to the variety of morphologies, quality of the fossil record and the enigmatic nature of these early plants, several hypotheses have been proposed for the affinities of *Cooksonia.* Edwards and Edwards (1986) placed *Cooksonia* in a group they called rhyniophytoids. Taylor (1988) termed the group cooksonioids, defined as small

plants with terminal sporangia borne on narrow axes that lack true tracheids, while other authors (e.g. Kenrick and Crane 1997) included *Cooksonia*-like axes in the Eutracheophytes.

Plate 6.1



Explanation of Plate 6.1

Cooksonia pertoni Lang; sporangia from the DBB at Weir Quarry, in lateral view. A) DBB.53.b; Aa) close up of A; B) DBB500.b; Ba) close up of B; C) DBB500.c; D) DBB6.53.4; E) DBB16.500.1; F) DBB15.500.1; G) DBB1.500.1; H) DBB5.53.4; J) DBB1.53; I) DBB4.53.5. Scale bars represent 100 µm for A-G, 20 µm for H and J and 10 µm for I.

Class Incertae sedis

Order Incerti ordinis

Family Incertae familiae

Genus HOLLANDOPHYTON Rogerson, Edwards, Axe and Davies, 2002

Type Species: *Hollandophyton colliculum* Rogerson, Edwards, Axe and Davies, 2002; from Ludlow, Shropshire, England.

Hollandophyton colliculum Rogerson, Edwards, Axe and Davies, 2002

Plate 6.2, Figures H-I

2002 *Hollandophyton colliculum* Rogerson, Edwards, Axe and Davies, p. 233, pls 1-4,

text-fig 1.

2004 *Hollandophyton colliculum*; Edwards and Richardson, p. 376, table 1, fig. 3. (d).

2004 *Hollandophyton colliculum*; Glasspool, Edwards and Axe p. 381, fig. 1.

2016 *Hollandophyton colliculum*; Hauser p. 64, fig. 4.

Holotype: NMW96.11G.7 Rogerson et al. 2002 (text fig. 1A; pl. 1, figs 2-5; pl. 2, fig. 6) from 160 cm above the Ludlow Bone Bed, at Ludford corner, Shropshire, England.

Material: 9 axes recovered using the paraffin expansion method (Hauser 2016) from the DBB at Weir Quarry.

Description: The axes all possess the same linear striations running parallel along their length. There are no sporangia present; however, there is a specimen (Plate 7.1, fig. L) that shows the upper part of the axis where the sporangia would have attached to the top of the axis. There is no clear evidence of any pores along the axes that are preserved.

Remarks: *Hollandophyton* was first described by Rogerson et al. (2002) from the PSM of Ludford Corner, Ludlow, from semi-compressed coalified fragmentary mesofossils. The spores of *Hollandophyton* are restusoid in nature in that the contact faces are delimited by changes in the density and the height of the ornament (Rogerson et al. 2002).

Genus SYNORISPORITES Richardson and Lister, 1969

Type species: *Synorisporites downtonensis,* recovered from Linton Quarry, Herefordshire, England.

Synorisporites downtonensis Richardson and Lister, 1969
Plate 6.3, Figure A

1969 *Synorisporites downtonensis* Richardson and Lister, p. 232, pl. 40, figs 4-5.
1996 *Synorisporites downtonensis*; Edwards et al. p. 784, pl. 1, figs 1-9.

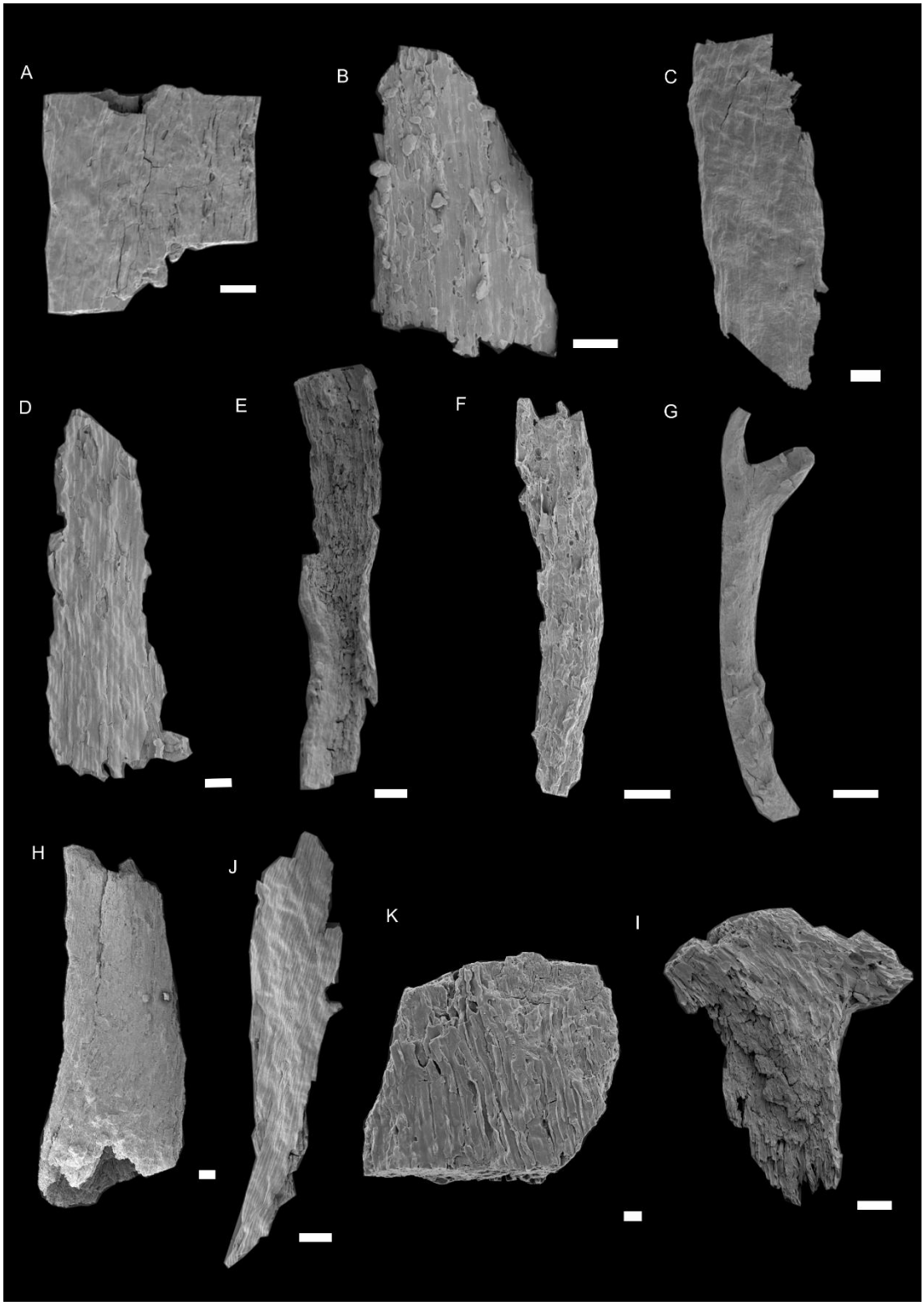
Holotype: Slide WB 32, ref. 3991063; housed in the Department of Geology, Kings College London; recovered from the "Lower Downtonian" at Linton Quarry (Richardson and Lister 1969).

Material: 1 partial sporangium, preserved in 3D with spores in place, recovered from HCL-HF-HCL processing of the DBB from Weir Quarry.

Description: Unlike the other sporangia in the DBB, that of *S. downtonensis* appears to be elongate (Plate 6.3, fig. A). Due to the breaks, it is unclear from where along the length of the sporangium the specimen is from. There is no detail on the spores.

Remarks: When first recorded in Richardson and Lister (1969) the species was known only from spore material. Edwards et al. (1996) recorded its ultrastructure for the first time.

Plate 6.2



Explanation of Plate 6.2

Eutracheophytes and allies from the DBB at Weir Quarry. A-G Axes of *Cooksonia pertoni* Lang; H-I Axes of *Hollandophyton colliculum* Rogerson, Edwards, Axe and Davies? A) DBB14.500.1; B) DBB3.53; C) DBB5.500.2; D) DBB5.53.1; E) DBB5. 500.1; F) DBB6.53; G) DBB2.53.3; H) DBB5.500.2; J) DBB9.500.1; K) DBB2.53; I) DBB8.500.1. The scale bars represent 100 µm except for K where it is 20 µm.

Class NEMATOPHYTINA Strother, 1993

Order NEMATOPHYTALES Lang, 1937

Family NEMATOTHALLACEAE Strother, 1993

Genus NEMATOTHALLUS Lang, 1937

Type species: *Nematothallus pseudo-vasculosa* Lang, 1937 from Freshwater East, Pembrokeshire, Wales.

Nematothallus pseudo-vasculosa Lang, 1937

Plate 6.3, Figures B-G; Text figure 6.4

1937 *Nematothallus pseudo-vasculosa* Lang, p. 269, pl. 12, figs 83-87, pl. 13, figs 88-93.

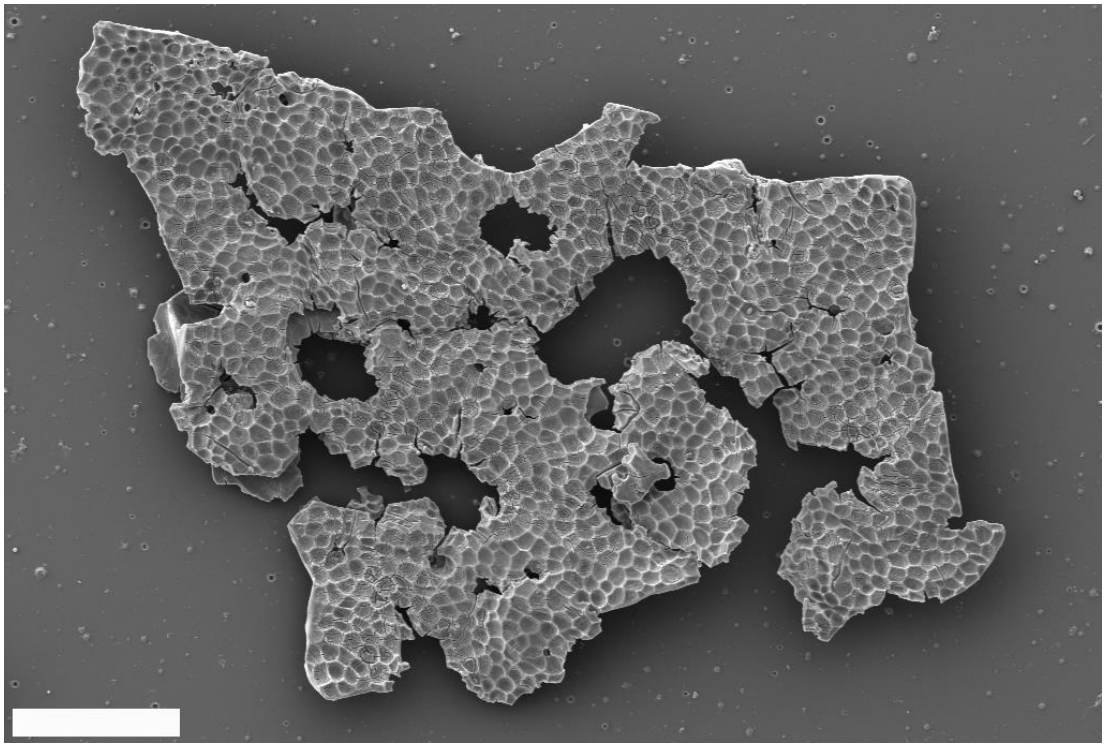
2013 *Nematothallus pseudo-vasculosa*; Edwards, Axe and Honegger, p. 506.

Lectotype: V54851 Designated by Strother (1993), as the specimen figured by Lang (1937, plate 12, figs 71, 75–80, 82). Film pull of original specimen, Natural History Museum, London.

Material: 29 specimens: 17 sheet-like structures and 12 3D structures, recovered from processing using the paraffin expansion method (Hauser 2016) and HCL-HF-HCL processing of the DBB from Weir Quarry.

Description: The sheet-like specimens are flat, although some are preserved with some 3D structures. The largest specimens are 1.5 mm across (Plate 6.3, fig. E); their surfaces are covered in venations which form cell-like structures (Text-fig. 6.4); some also have holes across the surface which are evenly distributed (Plate 6.3, figs B-C).

Remarks: *Nematothallus* has a range of morphologies. One example is similar to that described by Edwards et al. (2013) as a thallus with incised surfaces and emergent cortical protrusions. It has been suggested that *Nematothallus* represents the remains of leaf-like structures produced on *Prototaxites*-like axes (Corsin 1945; Jonker 1979). Despite this hypothesis, so far, no specimens in organic connection are known to support this. Although the true affinities of *Nematothallus* remain enigmatic, its affinities likely lie with fungi (Edwards et al. 2013).



Text figure 6.4 DBB7.53.3 *Nematothallus pseudo-vasculosa* Lang showing cell-like structure. Scale bar represents 100 µm.

Class incertae sedis

Order PROTOTAXALES Hueber, 2001

Family PROTOTAXITACEAE Hueber, 2001

Genus *PROTOTAXITES* Dawson, 1859

Type Species: *Prototaxites loganii* Dawson 1859, from Gaspé Bay, Quebec, Canada.

Prototaxites sp.

Plate 6.3, Figures H-I

1937 *Prototaxites* sp. Lang, p. 259, pl. 10, figs 40-47.

Material: Three specimens recovered from HF processing the DBB at Weir Quarry.

Description: Each specimen has different features. One shows a 'stem'-like structure which appears to be constructed from a mass of tubes (Plate 7.3, fig. H), while another is flat, the surface being covered by a cellular-like structure (Plate 7.3, fig. I); however, the 'walls' are much thicker than those seen in the *Nematothallus pseudo-vasculosa* specimens found in this study.

Remarks: Determining the affinities of *Prototaxites* has proved very difficult, and many different suggestions have been made. It was considered to be conifer wood by Dawson (1859), while later it was reinterpreted as being more algal-like and was transferred to another genus (*Nematophychus*) and then formally classified with the Codiaceae (green algae). It has also been compared to the brown alga *Lessonia* (Carruthers 1872; Kräusel 1936). However, when pores were studied on other specimens, the pores were like those seen in the pores and pit connections found in certain red algae. However, similar structures occur also in fungi (e.g. Basidiomycetes) in the form of dolipore septa. In some of the tubes or hyphae, small outgrowths occur close to the septa that resemble basidomycetous clamp connections (Hueber 2001). Added to this morphological data is chemosystematic work (Taylor et al. 2009) which again supported the affinity with algae, but the presence of cutin and suberin in the samples implied that the organism might have been terrestrial.

These, along with other biomarkers, have been used to hypothesize that *Prototaxites* could have been an "experiment" during early terrestrialization (Abbott et al. 1998). This was what Lang (1937) had initially suggested; it may belong to one of the several algal groups which were in the process of adapting to a terrestrial habit during the late Silurian but failed to survive to the present time (Niklas and Smocovitis 1983). Another interpretation of *Prototaxites* has been offered by Schweitzer (1983, 1990) based on a reinterpretation of *Mossellophyton hefteri*, a large, irregularly branched axis from the Lower Devonian of the Mosel Valley in Germany (Wehrmann at al. 2005), which was initially interpreted as a tracheophyte (Schaarschmidt 1974). This alga is believed to have inhabited shallow, tidally influenced coastal marine waters where it was attached by a root-like holdfast. More recently, however, a branched *Prototaxites* specimen was discovered in the Waxweiler quarry in Germany and interpreted as a portion of the basal holdfast of this organism (Schweitzer 2000). Despite this, it should be recognised that *M. hefteri* and *Prototaxites* have never been found in organic connection, and it remains questionable as to whether they belong to a single organism.

Class Incertae sedis

Order Incerti ordinis

Family Incertae familiae

Genus PACHYTHECA Hooker, 1853

Pachytheca sphaerica Hooker, 1853

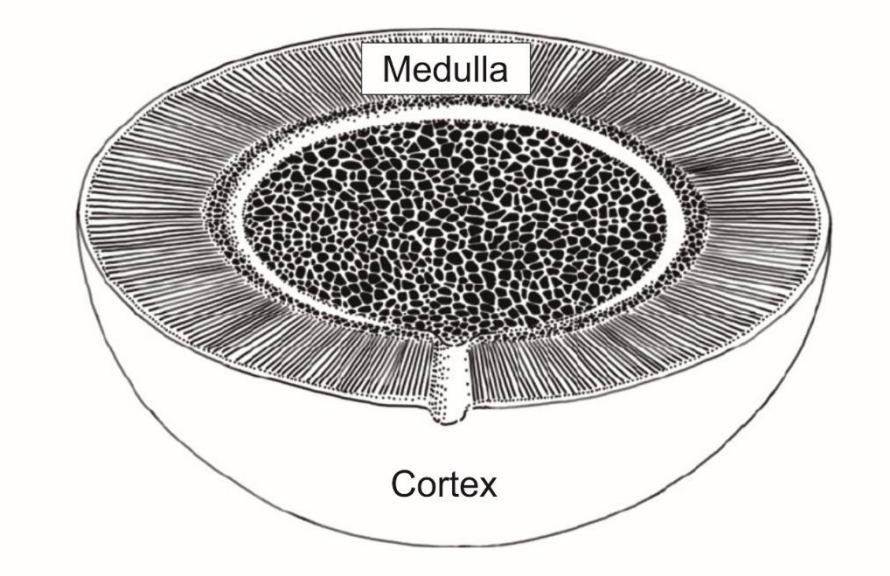
Plate 6.3, Figures J-K

1853 *Pachytheca* Hooker (in Strickland 1853), p. 12, figs 1-3.
1898 *Pachytheca*; Barber, p. 141, pl. 11, figs 1-14.
1937 *Pachytheca*; Lang, p. 275, pl. 14, figs 110-124.
1991 *Pachytheca*; Gerrienne, p. 267, pl. 1, figs 1-7, pl. 2, figs 1-6.
2004 *Pachytheca*; Edwards and Richardson, p. 383.

Holotype: It is unclear whether type material has been selected; however, the NHM in London does have several specimens collected by W. H. Lang. One specimen in the collection from the LBB at Saltwells, Dudley, England (PB V 57895) could be selected as a neotype as it is currently held in the NHM London and is referred to Strickland's paper.

Material: 4 incomplete specimens recovered from processing using the paraffin expansion method (Hauser 2016) on the DBB at Weir Quarry.

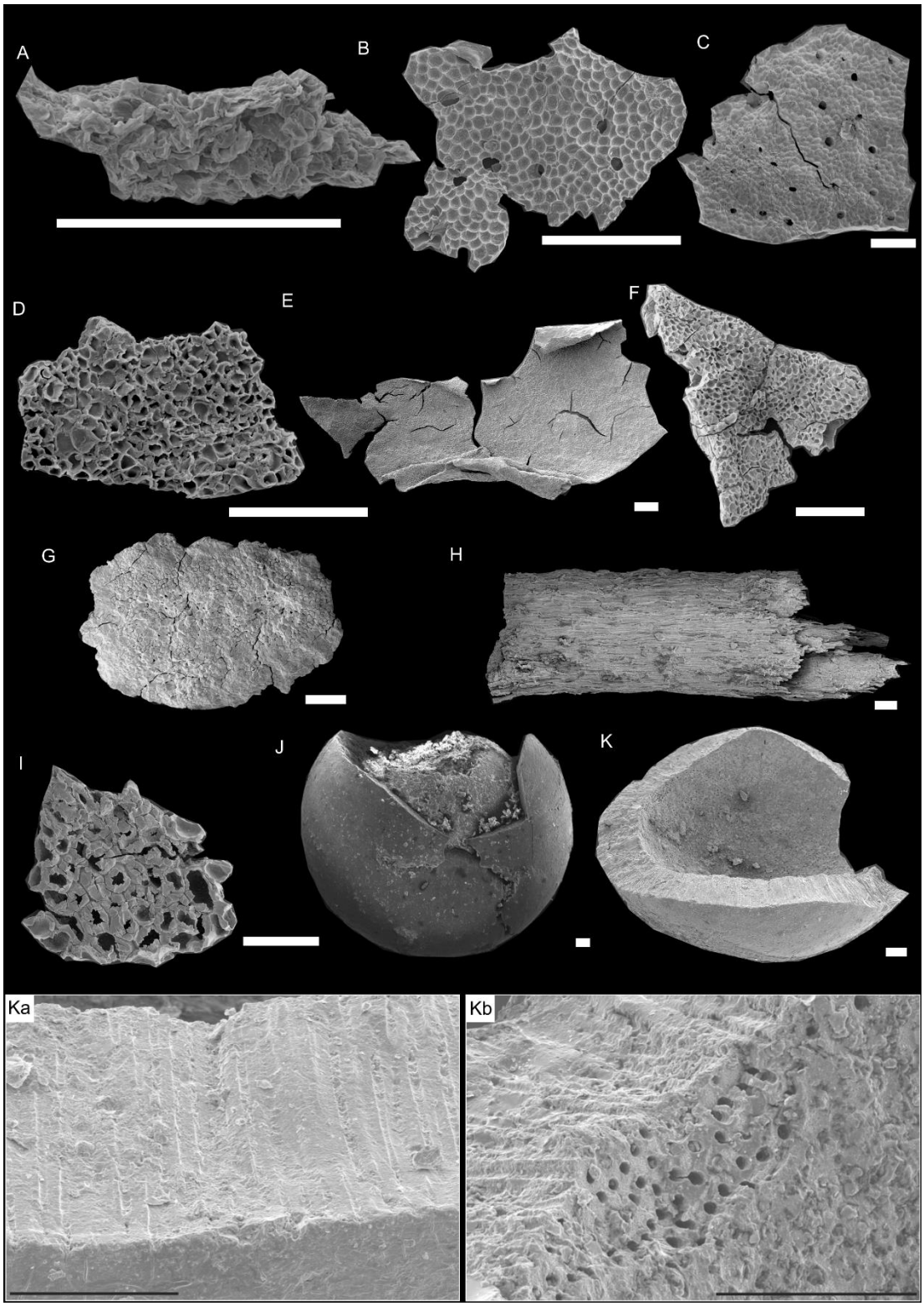
Description: *Pachytheca* are spheroid fossils that have thick walls (approx. 120 µm); on one broken specimen (Plate 6.3, fig. K) the structure of this fossil can be seen. It is made up of tubes that run from the inside of the fossil, known as the medulla, to the outside, known as the cortex (Text-fig. 6.5).



Text figure 6.5 Structure of *Pachytheca sphaerica* (modified from Taylor 1988).

Remarks: *Pachytheca* has repeatedly been interpreted as a dispersal unit (cystocarp) of *Prototaxites* (Schmidt 1958; Jonker 1979; Schweitzer 1983). Despite this, no organic connection has been found between the two so far. It has also been suggested that *Pachytheca* is merely the juvenile form of the taxon *Parka decipiens* and that the two taxa are simply the different ontogenetic stages of a single organism. Graham et al. (2004) conducted experiments that showed the extant liverworts (Kodner and Graham 2001) *Marchantia* and *Conocephalum* at various stages of controlled tissue degradation. The results showed that a number of these enigmatic nematophytes might represent the remains of ancient liverworts at various stages of decay. This may suggest that certain characters in some modern groups of liverworts may have persisted during the evolution of the group.

Plate 6.3



Explanation of Plate 6.3

Eutracheophytes and nematophytes found in the DBB at Weir Quarry. A *Synorisporites downtonensis* Richardson and Lister? B-G *Nematothallus pseudo-vasculosa* Lang H-I *Prototaxites* sp. J-Kb *Pachytheca sphaerica* Hooker.
A) DBB.53.d; B) DBB.53.I; C) DBB6.53.11; D) DBB6.53.6; E) DBB2.500.41; F) DBB7.53; G) DBB5.53.3; H) DBB.500.a; I) DBB8.53; J) DBB20.500.2; K) DBB20.500.1; Ka) DBB20.500.1a close up of K; Kb) DBB20.500.1c close up of K.
The scale is 100 µm for A-C, E, H, J-K. 20 µm for D, F-G, I and Ka, 10 µm for Kb.

PHYTOCLAST

Plate 6.4, Figure A

Material: 1 isolated specimen recovered from HCL-HF-HCL processing of the DBB from Weir Quarry.

Description: A tube-like structure that has a ridged 3D appearance approx. 10 µm wide (Plate 6.4, fig. A), akin to a segmented worm.

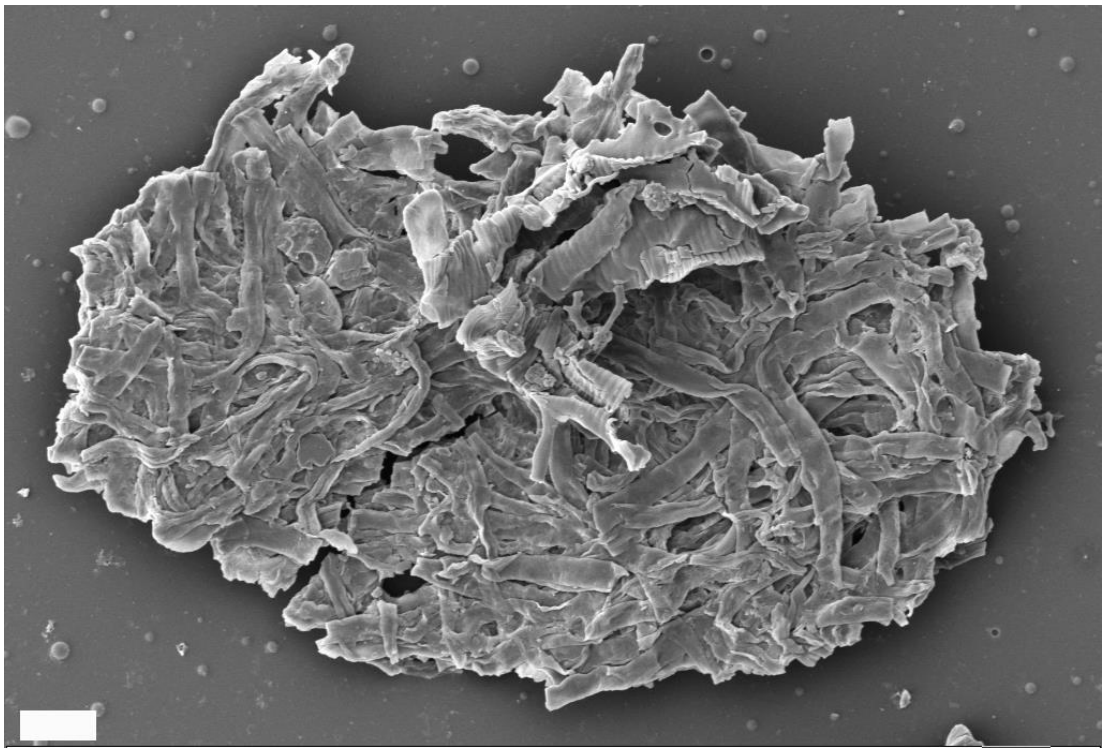
Remarks: These are referred to in the literature as banded tubes (e.g. Richardson and Rasul 1990); their affinities are unclear.

POSSIBLE FUNGAL HYPHAE

Plate 6.4, Figures B-C; Text figure 6.6

Material: 9 specimens recovered from HCL-HF-HCL processing the DBB from Weir Quarry.

Description: Mats of interwoven fibres (Plate 6.4, figs B-C Text-fig. 6.6) with few features except for their morphological similarities to fungal hyphae, which have potentially become flattened. It is unlikely that this is modern contamination as the example shown in Text-fig 6.8 has fragments of partial phytoclasts attached.



Text Figure 6.6 Close up of possible fungal mat from DBB at Weir Quarry.

UNIDENTIFIED ORGANIC MATERIAL

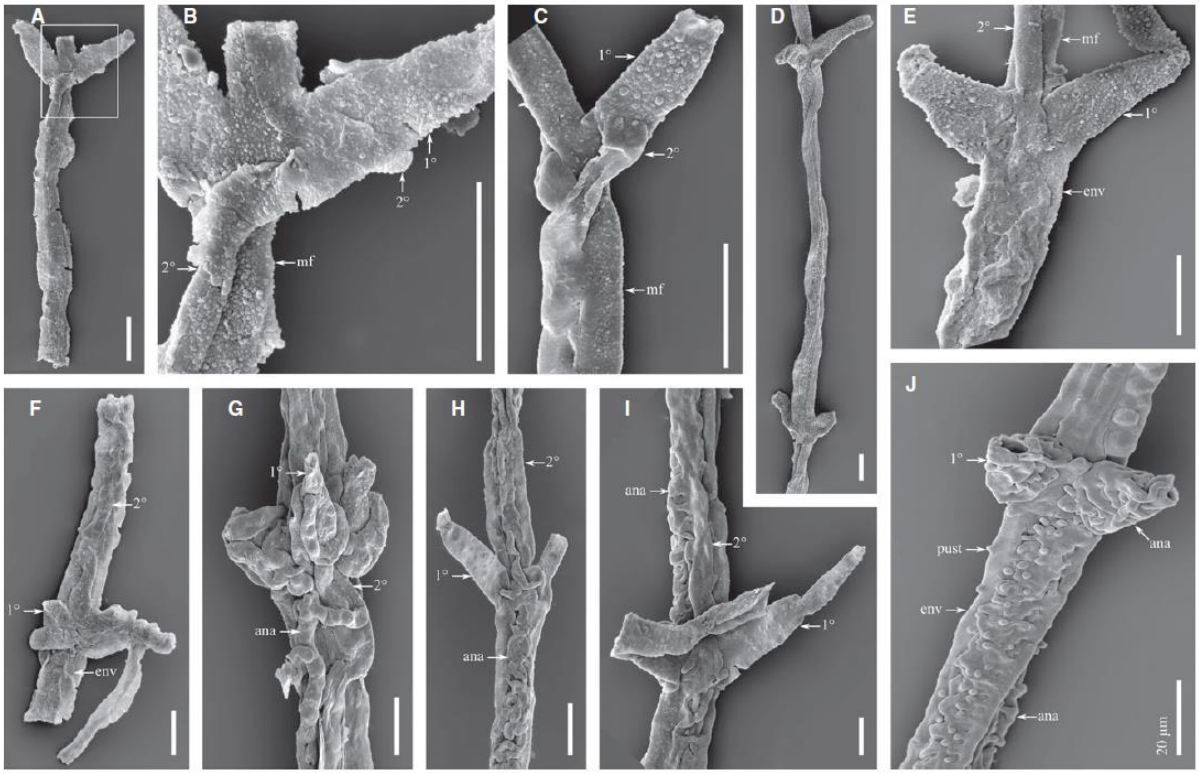
Plate 6.4, Figures D-J

Material: 21 fragments of unidentified organic material, recovered from HF processing the DBB at Weir Quarry.

Description: Various organic fragments of different morphologies and sizes were encountered: long tubes (Plate 6.4, figs D and E), with a needle-like appearance (D) with openings across their surface associated with swellings. Size ranges from ≥1,300 µm to ≥ 610 µm. Plate 6.4 figs F and G show small ≥ 100 µm to ≥190 µm specimens which have a structure. F, in particular, has almost a cusp-like appearance, although it also has pitted surface, whereas G has no specific features, a smooth surface and a "body" that tapers to a point, which appears broken. Plate 7.4, fig. H shows a cluster of 6 spherical bodies ≥130 µm across with each spheroid ≤20 µm across. Plate 6.4, fig. I is an amorphous specimen with some detail on the surface; irregular cell-like features with small circular structures across the surface. The specimen is approximately 340 µm across. Plate 6.4, fig. J shows a sheet-like

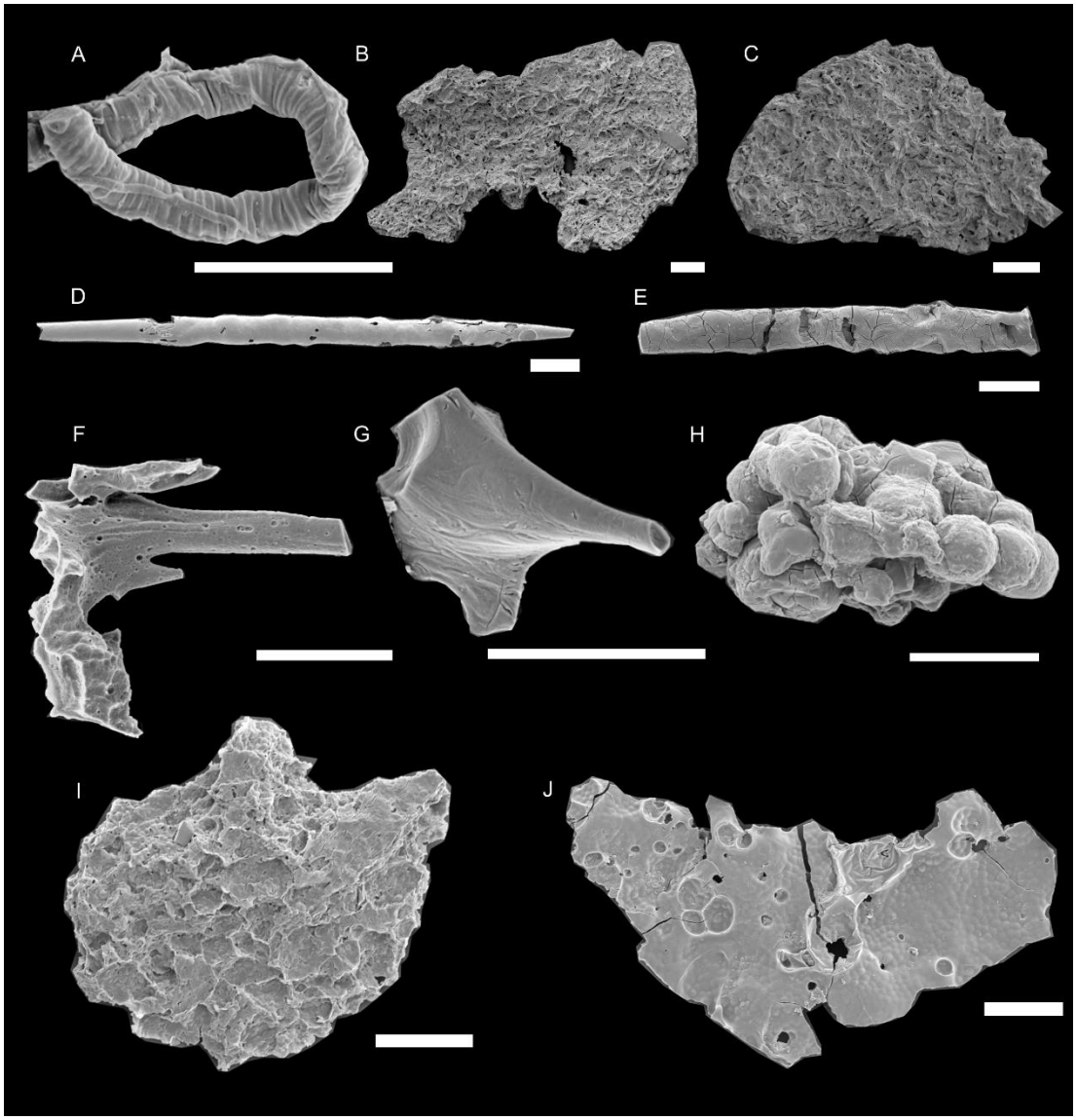
specimen, with dimpled ornamentation across the surface; it also shows what appears to be blistering. It measures c. 650 µm across.

Remarks: Although it was not possible to identify these specimens, Richardson and Rasul (1990) recorded a significant number of unidentified structures in what they referred to (p. 681) as dispersed organic material (D.O.M.) at the same horizon in Weir quarry. They also refer to a fungus known as *Tortotubus* (Text-fig. 6.7). Although this has some similarities to the tubes extracted from the DBB, *Tortotubus* is seldom straight and is often branching and appears to have surface ornamentation in the form of dimples (Smith 2015).



Text Figure 6.7 *Tortotubus* from the Burgsvik Formation, Gotland (taken from Smith 2015, fig. 5)

Plate 6.4



Explanation of Plate 6.4

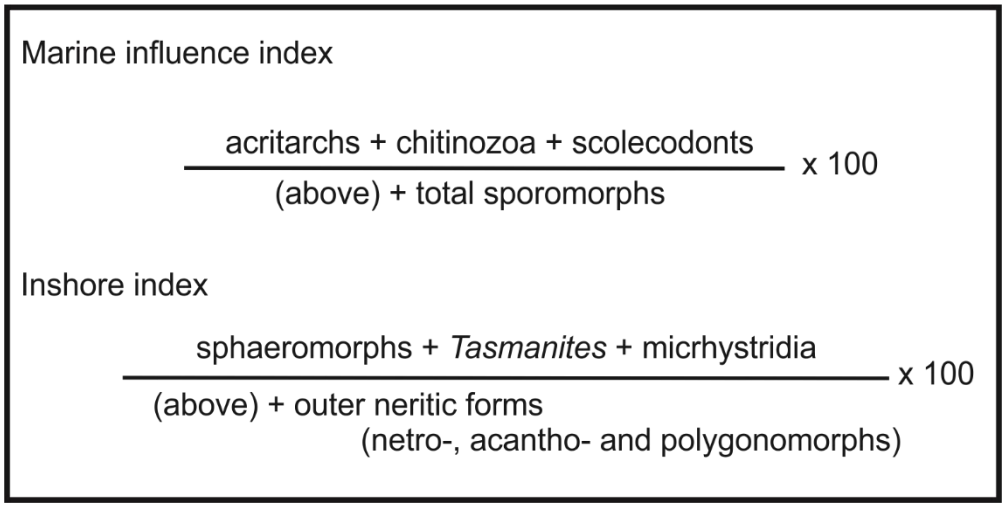
Organic-walled fossils from the DBB at Weir Quarry A, phytoclast, B-C possible fungal hyphae, D-J unidentified material. A) DBB10a.53; B) DBB2.500.11; C) DBB13.500.1; D) DBB3.53.7; E) DBB7.53.4; F) DBB4.53.6; G) DBB9.53; H) DBB7.53.7; I) DBB5.53; J) DBB2.53 The scale is 10 µm for A, F-H, 100 µm for B-E and J, 20 µm for I.

6.4 Discussion

This discussion of the plants and their allies is related to what insights they can provide to the palaeoenvironmental setting that the DBB formed in. As has been mentioned above in the taphonomy section, many of the plants preserved in the DBB from Weir Quarry are terrestrial; this, of course, means that they are all allochthonous. They can, however, still inform on the broader ecosystem that surrounded the Downton Sea during the late Silurian.

6.4.1 Richardson and Rasul's (1990) study

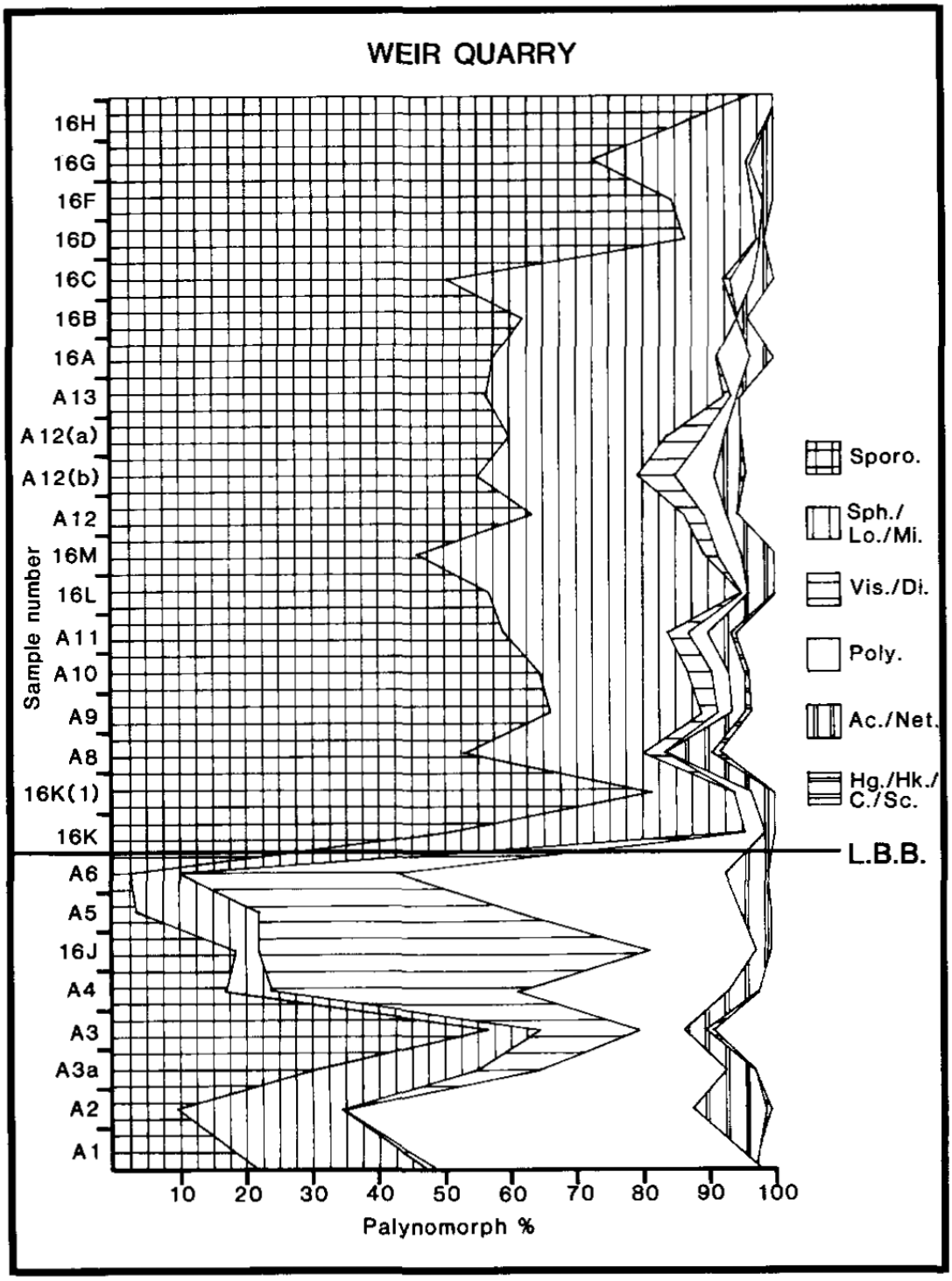
There are few direct studies of the Weir Quarry section. However, Richardson and Rasul's (1990) '*Palynofacies in a Late Silurian regressive sequence in the Welsh Borderland and Wales*' is an important paper because it provides an in-depth study on the palynology of Weir Quarry and other sections and provides an environmental interpretation based on their findings. As the title suggests, one of the key aims of the paper was to establish where in relation to the regressive sequence of the late Silurian various key sites were. To help determine this, they developed a marine influence index (M.I.I.), and an inshore index (I.I.) expressed by the formulae below (Text-fig. 6.8).



Text figure 6.8 The formulae used by Richardson and Rasul (1990) to calculate their index values.

At Weir Quarry, they collected 27 samples through a 7 m section through the UWF and the members of the DCSF. The samples of most importance to this study are samples 16C and 16D, which are taken through a bone bed that they recorded (Text-fig. 6.9). This bonebed is not the DBB, as it is recorded too high in the sequence (1.81-1.87 m above the LBB), it possibly relates to Bed 5 in the log (Text-fig 3.18). They note distinct changes taking place at the level of the LBBM and near the top of the PSM. In the DCSF they record the percentage of spores increasing across the UWF/Downton Group boundary from 2.5 % to 50.5 % before reaching a maximum of 80 %. It then declines before increasing rapidly samples 16C-16D (16D is within the PSM, while 16F is the lowest part of the Sandstone Member) from 51.5 % to the second peak of 86.5 % and remained high to the top of the section (72.5-87.5 %). The I.I. for the Downton Group is between 67.6 % and 96 %, which is in contrast with the upper metre of the underlying UWF, the index value for which was below 33 %. Spore percentages range between 50.5 % and 87.5 % in the DCSF; the percentages for most acritarchs are in single figures. Within the DCSF Micrhystridia (a loose association of polygonomorphs and acanthomorphs) are the only common acritarchs in the LBB and PSM. However, their occurrence becomes erratic in the Sandstone Member, while prasinophycean 'cysts' are the only common marine palynomorphs recorded, ranging from 8.5 % to 38.5 % of the total palynomorphs.

Richardson and Rasul (1990) also reported the presence of reworked acritarchs and sporomorphs of Tremadocian age, and also undifferentiated Ordovician or early Silurian age. In the PSM they show that its lower 1 m shows a strong but variable marine influence. However, there is a dramatic decrease in the M.I.I. from 49.7 % to 12.2 % between samples 16C and 16D near the top of the PSM. They reported that reworked acritarchs (acanthomorphs/netromorphs) are relatively common in the lower 36 cm of the PSM. However, they suggest that penecontemporaneous reworking is not thought to be the significant influence in the shift seen between samples 16C and 16D. This is because *Visbysphaera* was not observed in the counts of samples 16C and 16D, even though it was found in moderate abundance in the underlying samples from the UWF.



Text figure 6.9 Variation in palynomorph abundances (%), Weir Quarry section, near Downton. Sample levels are not to scale. Sporo., sporomorph; Sph./Lo./Mi., sphaeromorphs *Lophosphaeridium*/*Micrhystridium*; Vis./Di.,*Visbysphaera*/'*Dictyotidium*'; Poly., polygonomorphs; Ac./Net., acanthomorphs/netromorphs; Hg./Hk./C./Sc., hoegispheres/herkomorphs/chitinozoans /scolecodonts. (taken from Richardson and Rasul 1990, fig. 5).

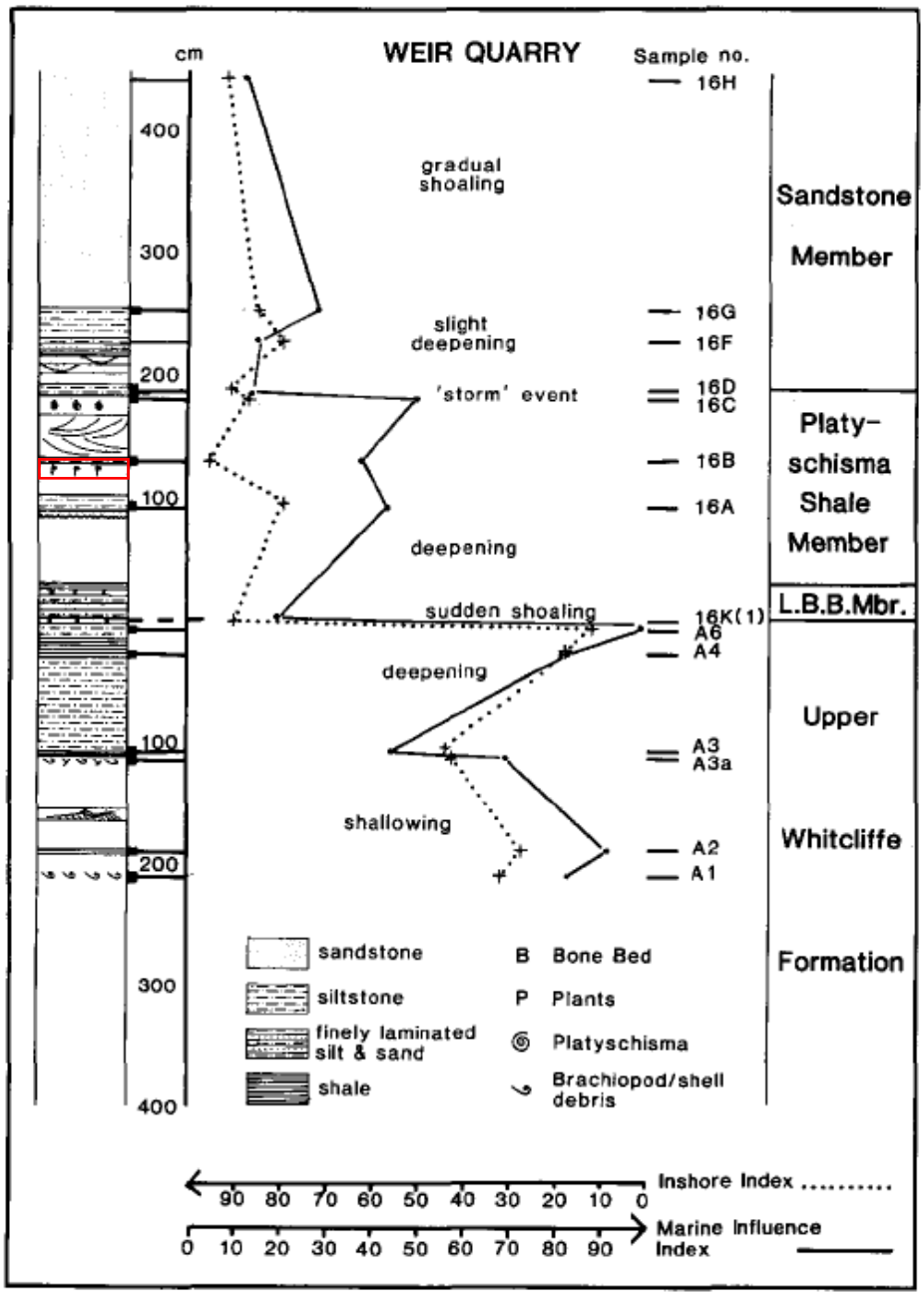
Richardson and Rasul (1990) also refer to changes that occur between samples 16C and 16D as the Platyschisma event, in which the M.I.I. reaches its second maximum in sample 16C and its minimum in 16D. Of interest is that they do not comment on whether they picked up the same signal at Ludford Lane. However, they do comment on several differences between the two localities (which are c. 5.5 km apart). These include a marked increase in the percentage, from 25.5% at Ludford Lane to 50.5%, while the samples from the Upper Whitcliffe Formation and the lower part of the Downton Castle Sandstone Formation at Weir Quarry had a lower proportion of acritarchs, the subgroups of which are primality regarded as outer neritic forms. Ricardson and Rasul (1990) regarded the variation in the results from the lowermost Downton Group samples between the Ludlow and the Downton areas, as being associated "to the pattern of distributary channels delivering high concentrations of land-derived sporomorphs in a nonuniform fashion along an irregularly prograding shoreline". Furthermore, samples from the UWF at Ludford Lane had "assemblages which indicate a greater land influence and a higher proportion of inshore microfossils than those from Weir Quarry" The reason for these differences is suggested by the authors possibly to be due to winnowing as many of the inshore acritarchs and prasinophytes are much smaller and more gracile than the more robust spores, so they suggest that they would have been preferentially removed and the spores would then become more relatively abundant. Throughout the lower Downton Group, they found that both mio/crypotospores are diverse but prasinophycean 'cysts' are the most common phytoplankton while acritarchs were generally rare or absent, except for *Micrhystridium*. *Visbysphaera* was rarely found and polygonomorphs and acanthomorphs were persistently present.

The reworking of Tremadoc and other Ordovician acritarchs as well as large, thick-walled tasmanitid prasinophytes and reworked, probably Llandovery, cryptospores (dyads and 'permanent' tetrads) were suggestive of a turbulent and erosive environment. They felt that it was difficult to determine how much of the acritarch assemblage represented undetectable late Silurian and therefore more or less penecontemporaneous reworking. Richardson and Rasul (1990) regarded the "Platyschisma event" as representing a storm event, simulating an offshore shift by bringing in material from the open sea. However, they felt that the real environmental shift was shoreward, as the underlying three samples indicated that

more marine conditions prevailed, whereas the higher samples generally show increasing terrestrial influence.

Richardson and Rasul (1990) also discussed the presence of dispersed organic material. They described the shale immediately overlying the bone bed as having: minor amounts of amorphous kerogen and some structured brown kerogen; small fragments of dark brown, thin unstructured cuticle (probably animal); structured animal and plant cuticle and banded tubes; branched unstructured tubes and more complex aggregations of tubes and filaments including fragments of *Tortotubus*.

Richardson and Rasul (1990) also made palaeoenvironmental interpretations based on their data; these were summarised for the section at Weir Quarry in their fig. 2 (Text-fig. 6.10). In the palynofacies curve, they show where they believe that there is evidence of shallowing, deepening, as well as a storm event. They also provide a summary of the palaeoenvironment, describing both the organic matter found and the environment that it represents (Text-fig. 6.11).



Text figure 6.10 Palynofacies curve for Weir Quarry, red box indicates position of DBB (copy of Richardson and Rasul 1990, fig. 2)

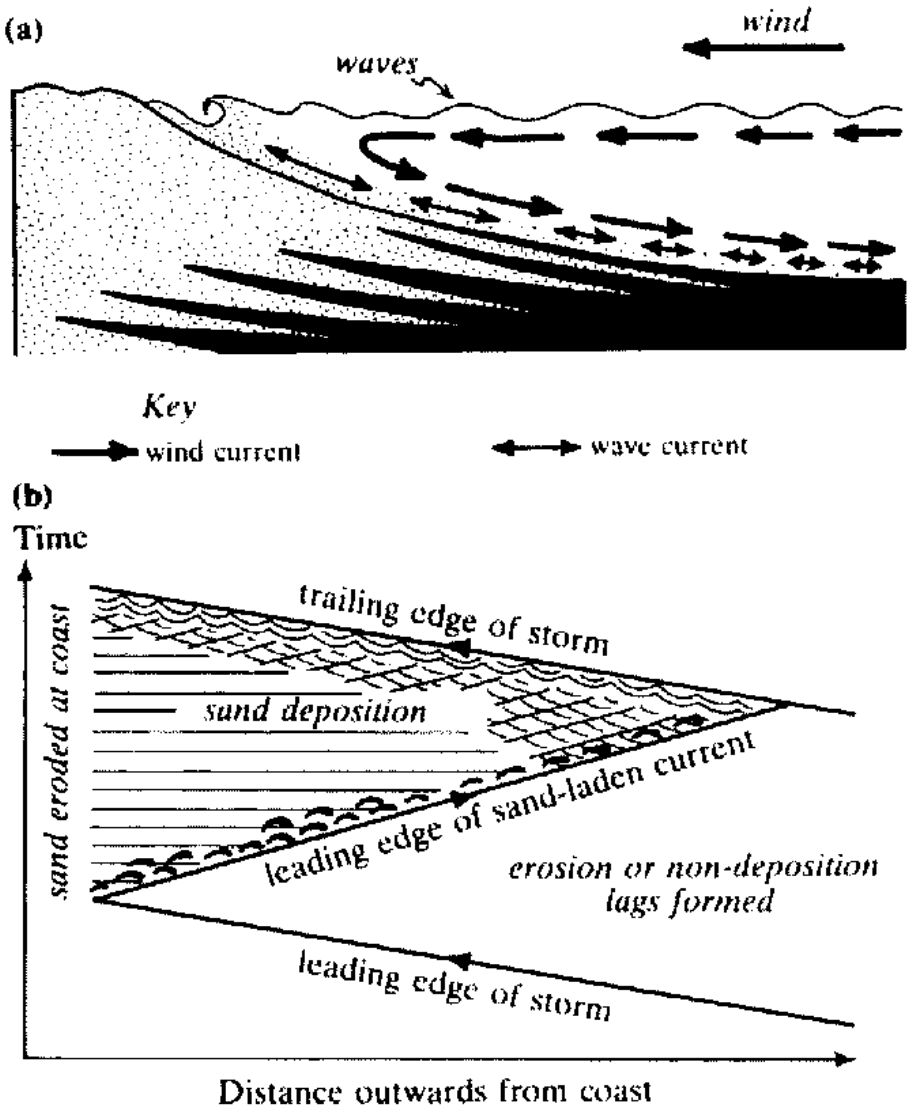
They described the PSM as representing "silts formed offshore within wave base". A response to the paper was published by Ainsworth (1991), who had previously co-published a short paper (Smith and Ainsworth 1989) on the presence of storm-formed sedimentary structures in the DCSF. Ainsworth suggested that caution should be taken in the interpretation of environment from palynological analysis in a storm dominated setting. Overall trends in palynofacies curves may reflect sea-level histories better than spikes within the data, which he suggested can be explained by

storm mixing and reworking of terrestrial and marine assemblages. In response, Richardson and Rasul (1991) agreed that palaeontology and sedimentology should be studied in concert when trying to interpret the effects of storm-influenced sequences on land-derived material and phytoplankton.

Organic matter	*Environment*
Temeside Shale Formation Very large cuticle fragments.	Subtidal & Intertidal: Sands of subtidal shoals and lower intertidal flats. Silts of upper intertidal flats. Strong waves and currents. Brackish and turbid water.
Downton Castle Sandstone Formation *Sandstone Member* Increase in large fragments of plant cuticle; lath-shaped (some long) and irregular vitrinite fragments; some banded tubes; brown and black unstructured 'filaments' sometimes in mats; sporangial masses.	Near-shore to beach: Strong waves, turbid, often brackish. Transgressive sand shoals and beaches.
Platyschimsa Shale Member Lath-shaped vitrinite fragments, and banded, 'scrolled' & smooth tubes become dominant; many large irregularly-shaped fragments of humic kerogen especially in the lower part of the member; mats of fine tubes or 'filaments'; plant cuticle more abundant in some samples from the upper part of the member (16A & 16C); sporangial masses. Large fragments of animal cuticle, some perforate.	Silts formed offshore within wavebase.
Ludlow Bone Bed Member Black vitrinite and brown humic material; lath-shaped fragments and smooth and banded tubes common, tubes variable in size, up to 400 μm long; narrow, 3–5 μm wide, yellow to brown, smooth tubes; black and brown irregular fragments; sheets, some perforate, mainly black, some brown; small fragments of plant cuticle; thin brown (probable animal) cuticle.	Near-shore to offshore: laminated silts and some thin sands.
Ludlow Bone Bed Irregular organic fragments (humic material) abundant; banded tubes and simple and branched filaments.	Advance of strand after retreat: beach and littoral sands and silts.
Upper Whitcliffe Formation (upper part of) Amorphous kerogen dominant, rare small fragments of plant/animal cuticle and banded tubes.	Chiefly open sea: clays and limestones formed chiefly within wavebase. Clear sea, often turbid, sometimes brackish. Periodic strand retreat and advance.

Text figure 6.11 Summary of organic matter found in the upper Silurian of the Welsh Borderlands and the interpreted environment (taken from Richardson and Rasul 1990, table 4).

Richardson and Rasul (1991) stated that Allen (1985 fig. 13.34; Text-fig. 6.12) provided a model of storm sedimentation whereby an onshore storm would provide net transport offshore. They suggested that under those conditions sporomorphs, sphaeromorphs and banded tubes, the abundance of which would usually indicate proximity to shore would be carried further out to sea, while also undergoing some form of sorting. It was suggested that this would produce the abrupt change seen in the "Platyschisma event".

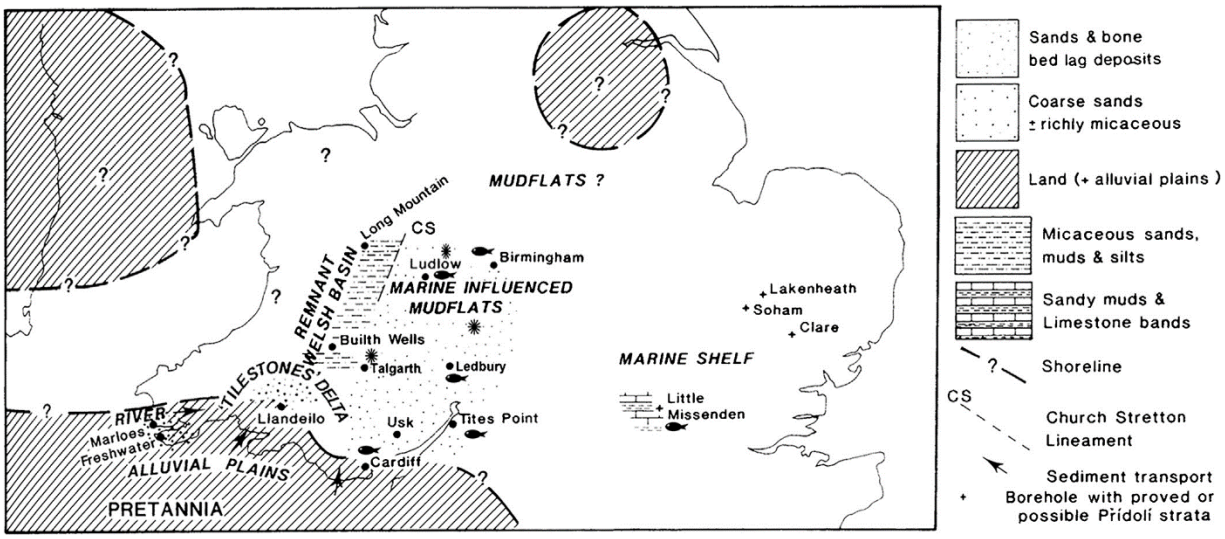


Text figure 6.12 storm sedimentation model suggested by Richardson and Rasul (1991) (taken from Allen 1985, fig. 13.34)

This discussion of the two papers (Smith and Ainsworth 1989 and Richardson and Rasul 1990) is useful when attempting to understand what the palaeobotanical evidence can suggest about the depositional setting of the DBB at Weir Quarry. The concept that storm activity can skew the evidence for proximity to land is important to the interpretation of the depositional setting of the DBB, because according to Richardson and Rasul (1990) the PSM formed within wave base. However, the sedimentological evidence from this study would suggest that the location of where the DBB was deposited was below fair-weather wave base. Thus, despite the palynological evidence suggesting a closer to shore proximity, due to storm activity, it may have been deeper.

6.4.2 Palaeoenvironment

Considering that Richardson and Rasul (1991) suggested that an onshore storm washed material out into the Downton Sea, where was the source of this terrestrial material, during the late Silurian? Siveter et al. (1989) established the presence of a delta complex referred to as the Tilestone Delta (Text-fig. 6.13); this then provides a model for the shoreline of the Downton Sea and a possible source for the terrestrial material.



Text Figure 6.13 Palaeoenvironments in the Welsh Borderland region during the late Silurian (taken from Turner et al. 2017 fig. 9).

There is one final observation and inference that can be made from the plant fossils, which relates to how they are preserved. As discussed in the preservation section of this chapter, it was established that the exceptional preservation seen in the plants is the result of low-temperature wildfires (Glasspool et al. 2004). However, this evidence of wildfires combined with climate interpretations made by Allen (1974), who suggested that the climate was warm to hot with seasonal rainfall, could be used to infer that during the late Silurian the Downton Sea was climatically seasonal with a dry and wet season. This could account for the desiccation (Glasspool et al. 2004) before storms which appears to have dominated the environment (Smith and Ainsworth 1989) which may have ignited the already dry plants, before further increased rainfall washed material offshore. Finding other examples of this in the fossil record is challenging not because of the lack of examples of fluctuating salinity in the fossil record (Arthur et al. 1983, Fürsich 1993, Brigaud et al. 2008, Nützel et al. 2010 and Crippa et al. 2016). It is because most studies use isotopic data from bivalve shells it monitor fluctuations in salinity, but as mentioned within Chapter 5 the shells of the bivalve *Modiolopsis complanata* have been lost thought diagenesis, so a comparative study of this nature in the DBB would not be possible.

7. Ichnology

7.1 Introduction

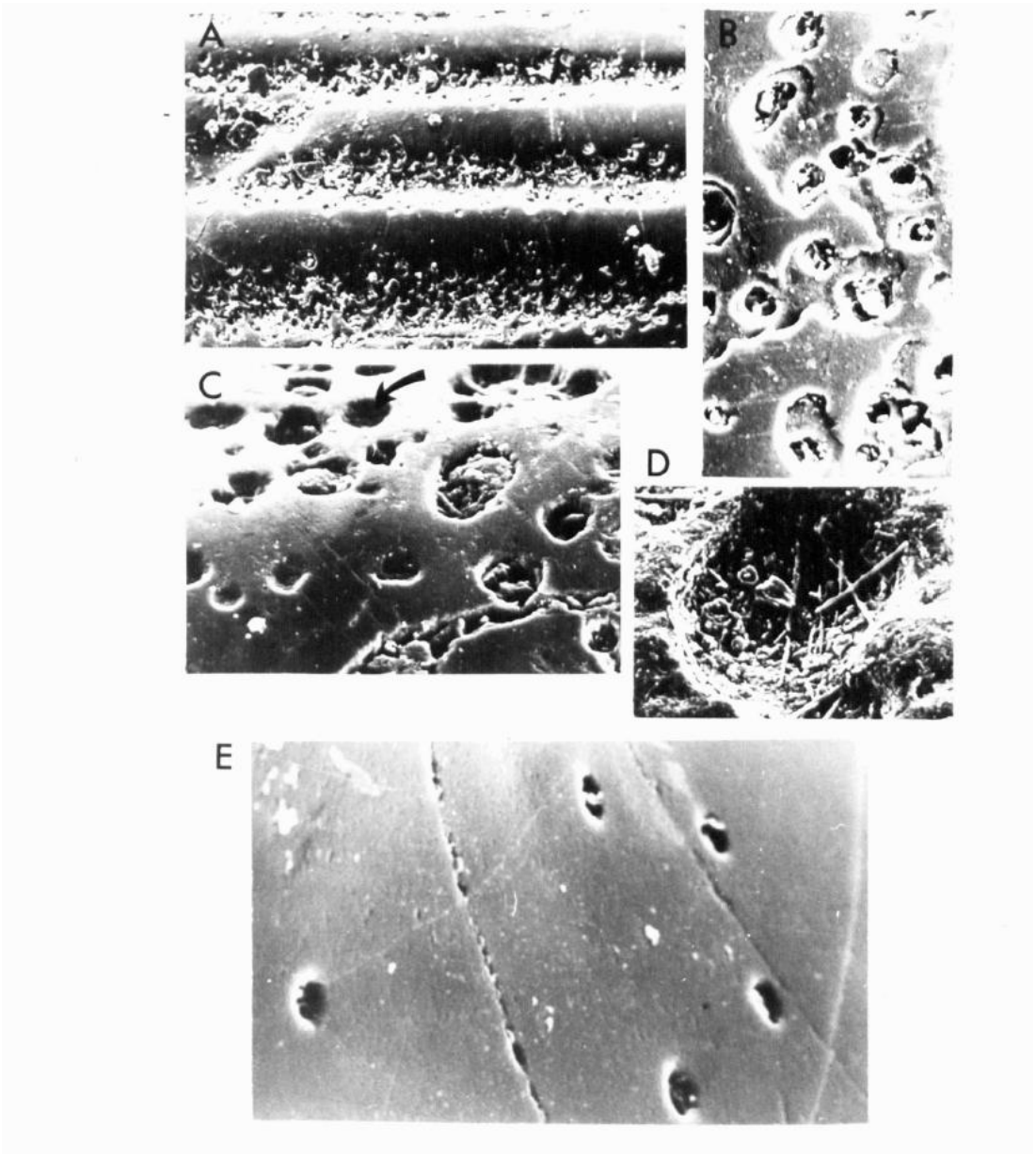
This chapter focuses on the trace fossils of the DBB at Weir Quarry. The chapter will describe previous work that is of relevance to this study. The preservation of the trace fossils will be briefly discussed. Descriptions of the trace fossils are provided in the style of the journal *Palaeontology*. Finally, there will be a discussion of the findings of this chapter.

7.1.1 Previous work

Despite the Downton Castle Sandstone Formation's long history of study, its trace fossils have remained almost entirely unstudied. Trace fossils, however, have been recorded from the LBB. Antia (1979) documented micro-borings in the denticles of the thelodont *Thelodus parvidens* (Agassiz, 1839) and the acanthodian *Gomphonchus tenuistriata* (Agassiz). He recorded these occurrences at five LBB sites (Ashton Munslow, Corfton, Rushall, Prior Frome and Ludlow). It is unclear what the organism was that produced the borings. Antia refers to Warne (1975, p. 196) which, he suggested, pointed to sponges producing the borings. He then suggested that various organisms could have produced them, but did not specify which ones. The microboring was named *Thelodontites corftonensis* (unpublished thesis), but this name has never been published. These have not been seen in the DBB at Weir Quarry most probably due to the differences in the bone bed's formation. It is suggested by Dineley and Metcalf (1999) that the LBB represents lag deposits within a very shallow subtidal to low intertidal environment, which may have been initially deposited during storm events (Smith and Ainsworth 1989) whereas the denticles within the DBB at Weir Quarry appear to have been buried before being exposed to any infestation by micro-bionts.

Since coprolites were first identified and named (Buckland 1829), they have given researchers insights not only into the physiology of the trace producer but also the diet of the trace maker, informing on the relationships between organisms within an

ecosystem. Coprolites provide some of the earliest evidence for animal-plant interaction and colonization of the land (Edwards et al. 1995). Some of the first recorded coprolite material from Silurian terrestrial animals came from the upper Silurian Burgsvik Sandstone of Sweden (Sherwood-Pike and Gray 1985). They recorded fungal hyphae within faecal pellets and proposed that they were produced by mycophagous microarthropods. Coprolites have also been recorded from the upper Silurian of the Welsh Borderlands recorded from three localities: North Brown Clee Hill, Ludford Lane and Perton Lane (Edwards et al. 1995). Edwards et al. (1995) are not specific about the section at Ludford Lane that the material came from, only that early terrestrial invertebrates have been found from the same bed. It is assumed here that they are referring to the LBBM. They suggested that they were produced by a spore eater, most likely a detritivore akin to modern millipedes. They were able to rule out that the specimens were isolated sporangia due to the regular shape, lack of enclosing sporangium wall, presence of more than one spore type (in one specimen they recorded as many as nine types) and presence of varying proportions of cuticles, tubes and less easily identifiable plant debris. A summary of early terrestrial animals and their traces was provided by Shear et al. (2001) who summarized the work carried out at Ludford Corner. Later Hagström and Mehlqvist (2012) described terrestrial invertebrate coprolites from the upper Silurian of Gotland from the Burgsvik Sandstone.



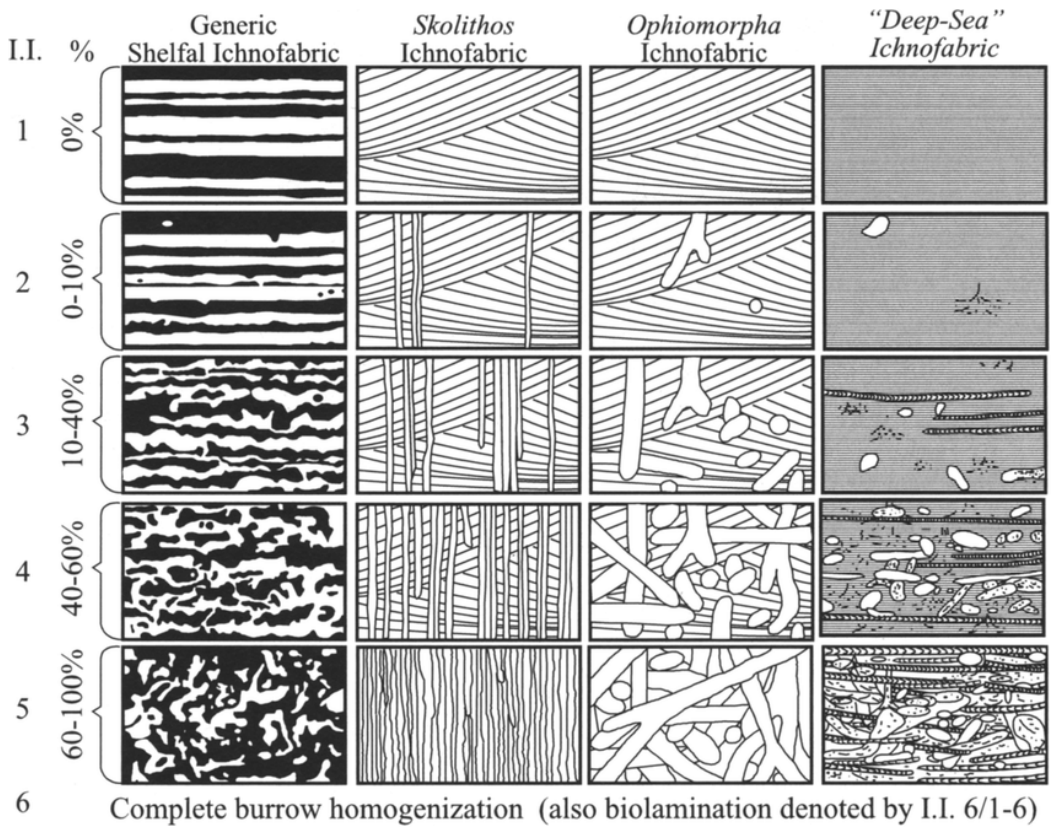
Text figure 7.1 Antia's plate 1 from his 1979 PhD thesis showing "*Thelodontites corftonensis"*. A) *Gomphonchus tenuistriata* fragment with "*T. corftonensis*" boring in its grooves. (Distance between adjacent grooves = 250-300 µm). B) Borings on a phosphatized fragment of *Serpulites* sp. (Boring diameter = 10-15 µm) C) "Holotype" of "*T. corftonensis*" (arrowed) on the illustrated (Plate 1A) specimen of *G. tenuistriata*. Recent *Thelodontites* boring (diameter 30 µm) from Sales Point, Bradwell, Essex. E) Algal form B boring of Antia (1979a) on a *Thelodus parvidens* scale. Note the weathering stage 1 cracks (cf. Antia, 1979a) diameter of borings = 10-15 µm.

7.2 Preservation

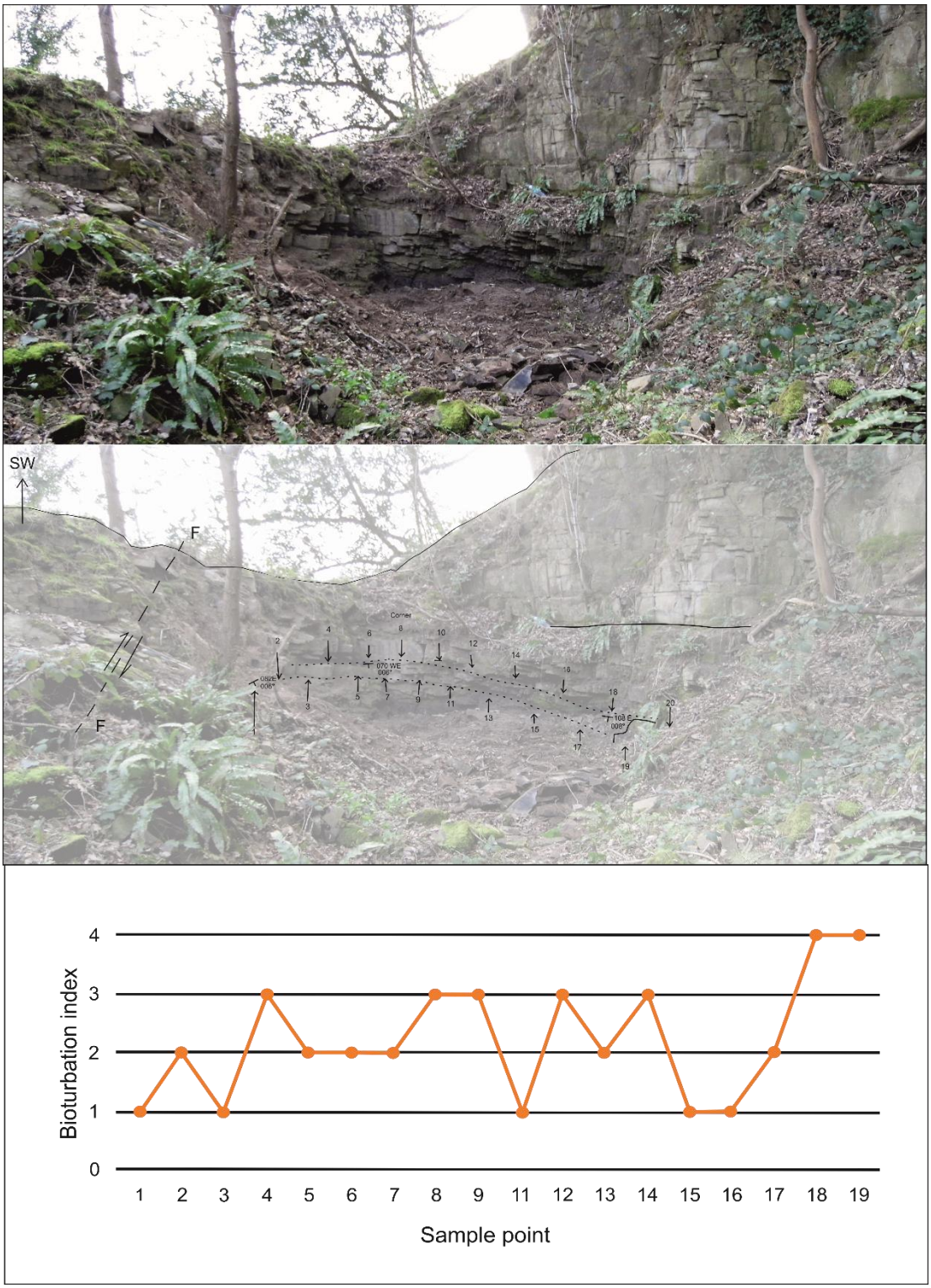
The trace fossils in the DBB are picked out by black outlines that are interpreted to represent oxidised organic matter or weathered pyrite, used in the burrow wall, e.g. a mucus layer that has formed pyrite as it decays. They are also highlighted by the difference in the grain size and mineralogy between the matrix and infill.
The possible coprolites are preserved similarly to the sporangia in the DBB at Weir Quarry. They appear carbonized, possibly from the same low-temperature fire, allowing them to survive bacterial decay.

7.3 Bioturbation index

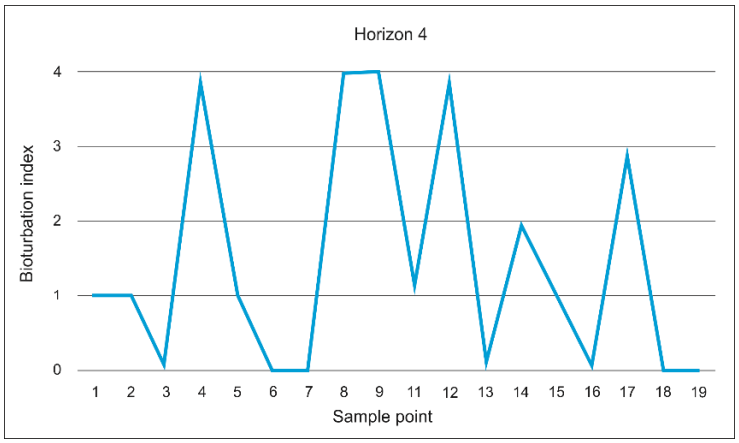
Due to the lateral variability of the DBB and the difficulty in accessing parts of the exposure to recover samples, the bioturbation index (B.I.) sometimes referred to as Ichnofabric Index (I.I) (Text-fig. 7.2.) has been looked at across the DBB at Weir Quarry except for sample point 10. To study the B.I. for the DBB at Weir Quarry, cut sections of each sample from the collection points at Weir Quarry's Bed 9 (the Downton Bone Bed) (Plate 7.1-Plate 7.6) were studied for its B.I. Variations in average B.I. are shown in Text-fig 7.3, with B.I. for each horizon of the DBB shown in Text-fig 7.4.

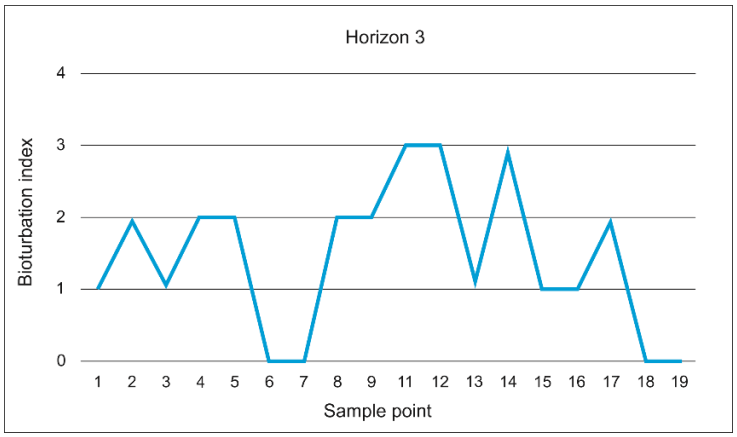


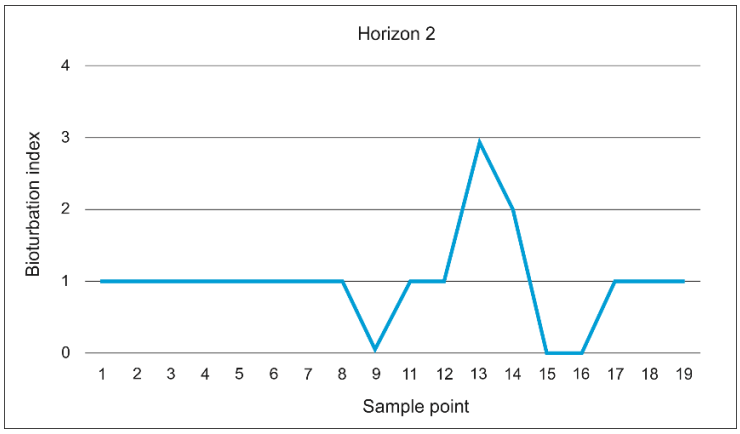
Text figure 7.2 Ichnofabric indices, indicating the amount of bioturbation (taken from Droser and Bottjer 1989).

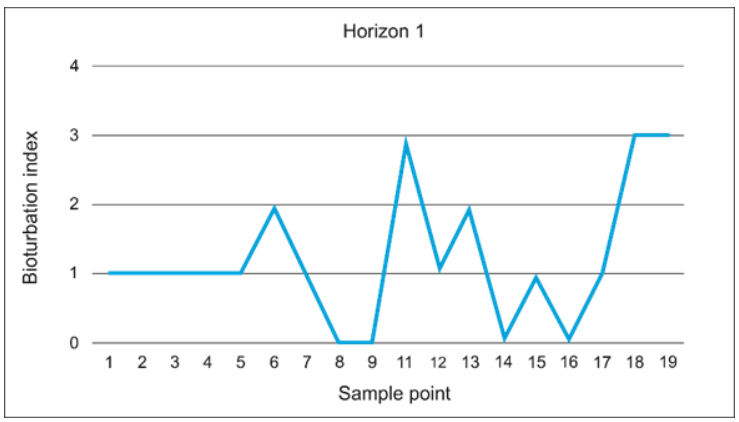


Text figure 7.3 Top: An image of the Weir Quarry section. Middle: overlay of sample collection points within the Weir Quarry section. Bottom: variation in bioturbation index of the DBB across the section. F= fault.



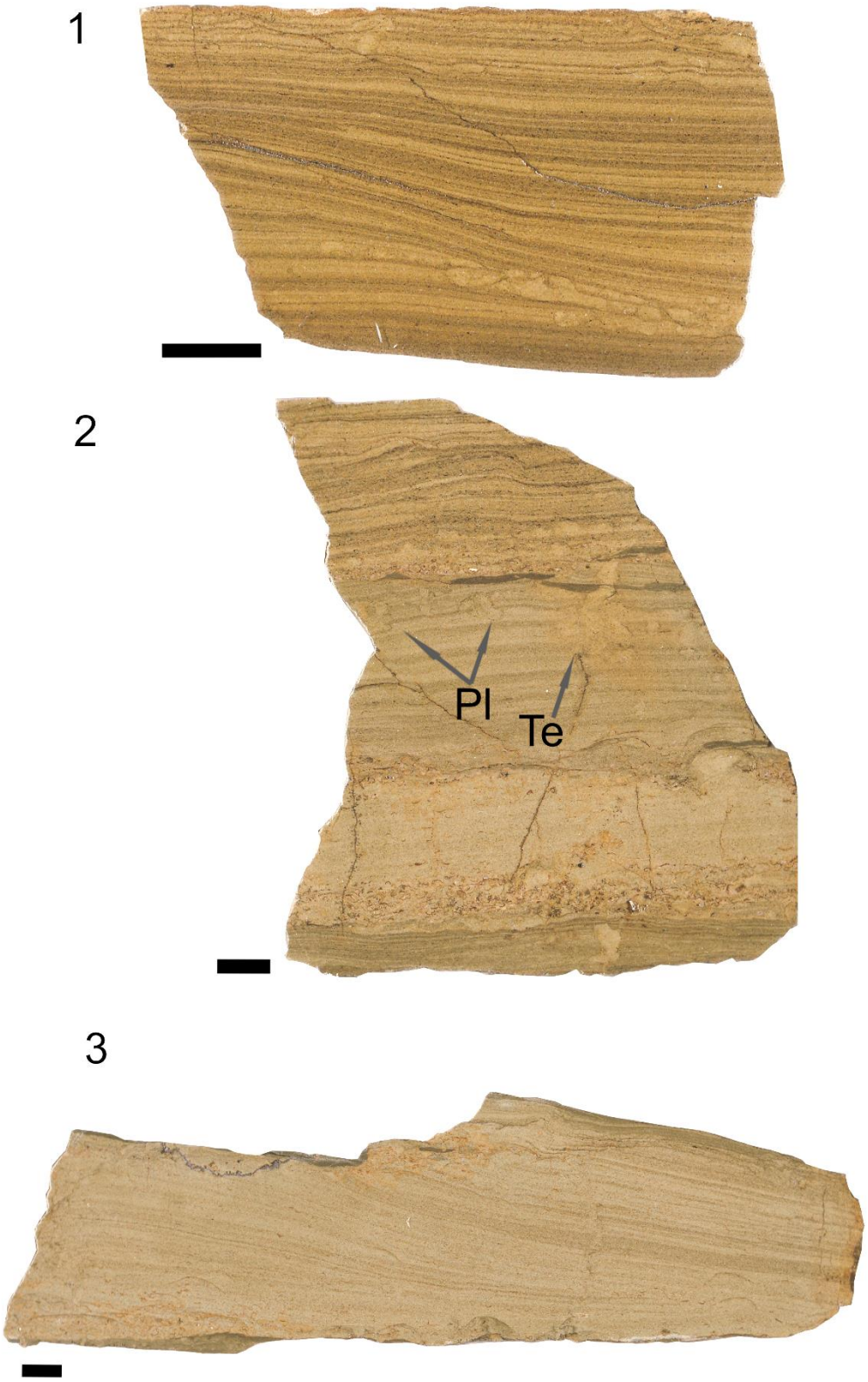






Text figure 7.4 Graphs of each horizon's B.I., across the 8 m of lateral exposure at Weir Quarry with the sample points 1-19; as only a small amount of 10 could be collected it is omitted.

Plate 7.1



Explanation of Plate 7.1

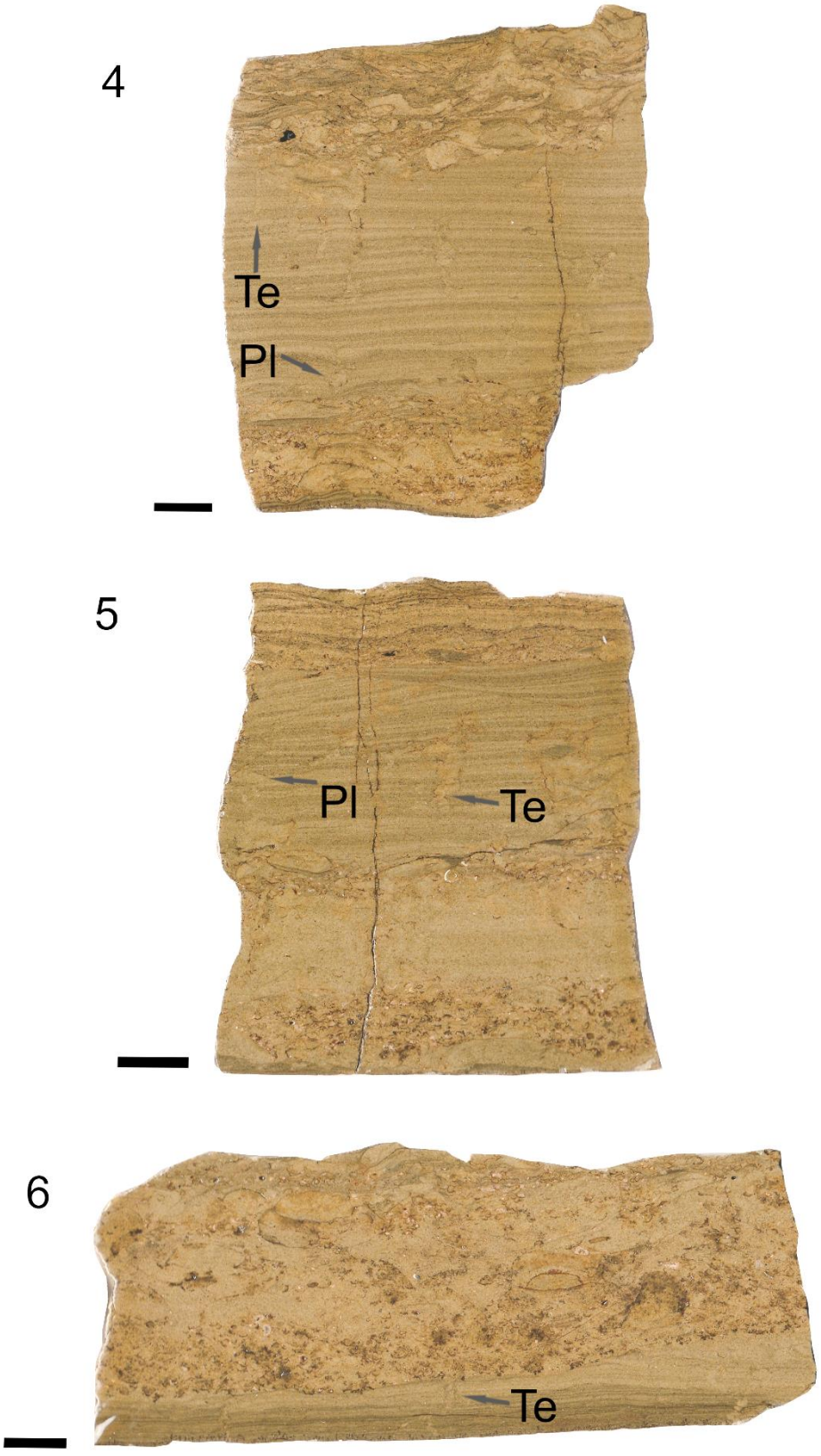
Cut sections of DBB at Weir quarry showing B.I., samples from collection points 1-3. The scale represents 1cm.

1) B.I. 1. No trace fossils present

2) B.I. 2. *Teichichnus* sp. (Te) is present in the middle of the bed, while *Planolites* sp. (Pl) can be seen in the top of the bed.

3) B.I. 1. No trace fossils present.

Plate 7.2



Explanation of Plate 7.2

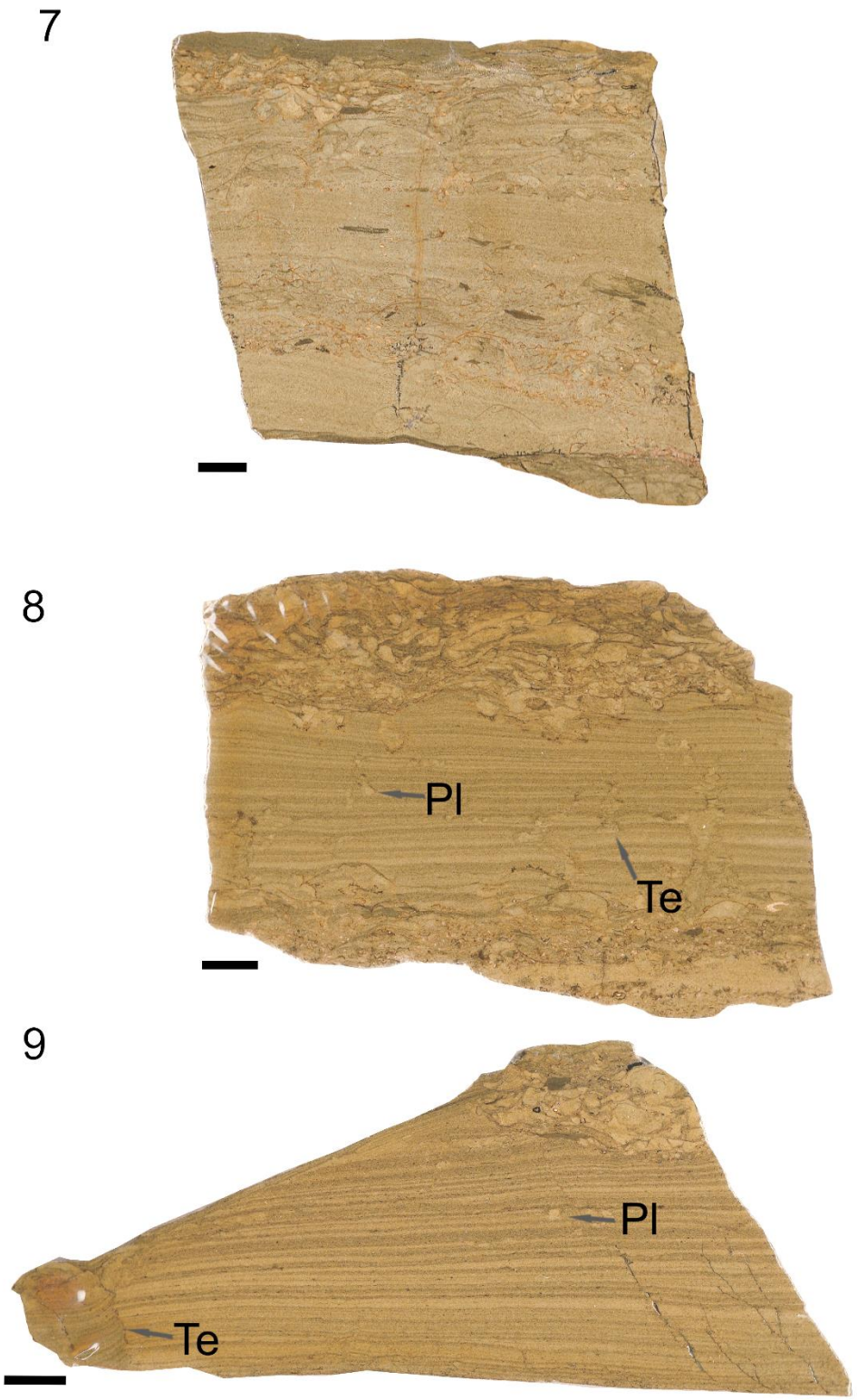
Cut sections of DBB at Weir quarry showing B.I., samples from collection points 4-6. The scale represents 1cm.

4) B.I. 3. *Teichichnus* sp. and *Planolites* sp. are present in the middle of the bed; the top of the bed shows extensive bioturbation.

5) B.I. 2. *Teichichnus* sp. and *Planolites* sp. are present only in the middle of the bed.

6) B.I. 2. *Teichichnus* sp. is present in the lower part of the bed.

Plate 7.3



Explanation of Plate 7.3

Cut sections of DBB at Weir quarry showing B.I., samples from collection points 7-9. The scale represents 1cm.

7) B.I. 2. Extensive bioturbation in horizons at top and bottom of the bed, No ichnogenera can be identified.

8) B.I. 3. *Teichichnus* sp. and *Planolites* sp. are present in the middle of the bed the top of the bed shows extensive bioturbation.

9) B.I. 3. *Teichichnus* sp. and *Planolites* sp. in the lower part of the bed, with a large example of *Teichichnus* sp. on the right-hand side, with clear spreiten structures. Extensive bioturbation at the top of the bed.

Plate 7.4

Explanation of Plate 7.4

Cut sections of DBB at Weir quarry showing B.I., samples from collection points 11-13. The scale represents 1cm.

11) B.I. 1. No trace fossils present.

12) B.I. 3. Extensive bioturbation is seen in the upper part of the horizon; no ichnogenera can be identified.

13) B.I. 2. Bioturbation is seen in the lower and upper parts of the bed, *Teichichnus* sp. present.

Plate 7.5

Explanation of Plate 7.5

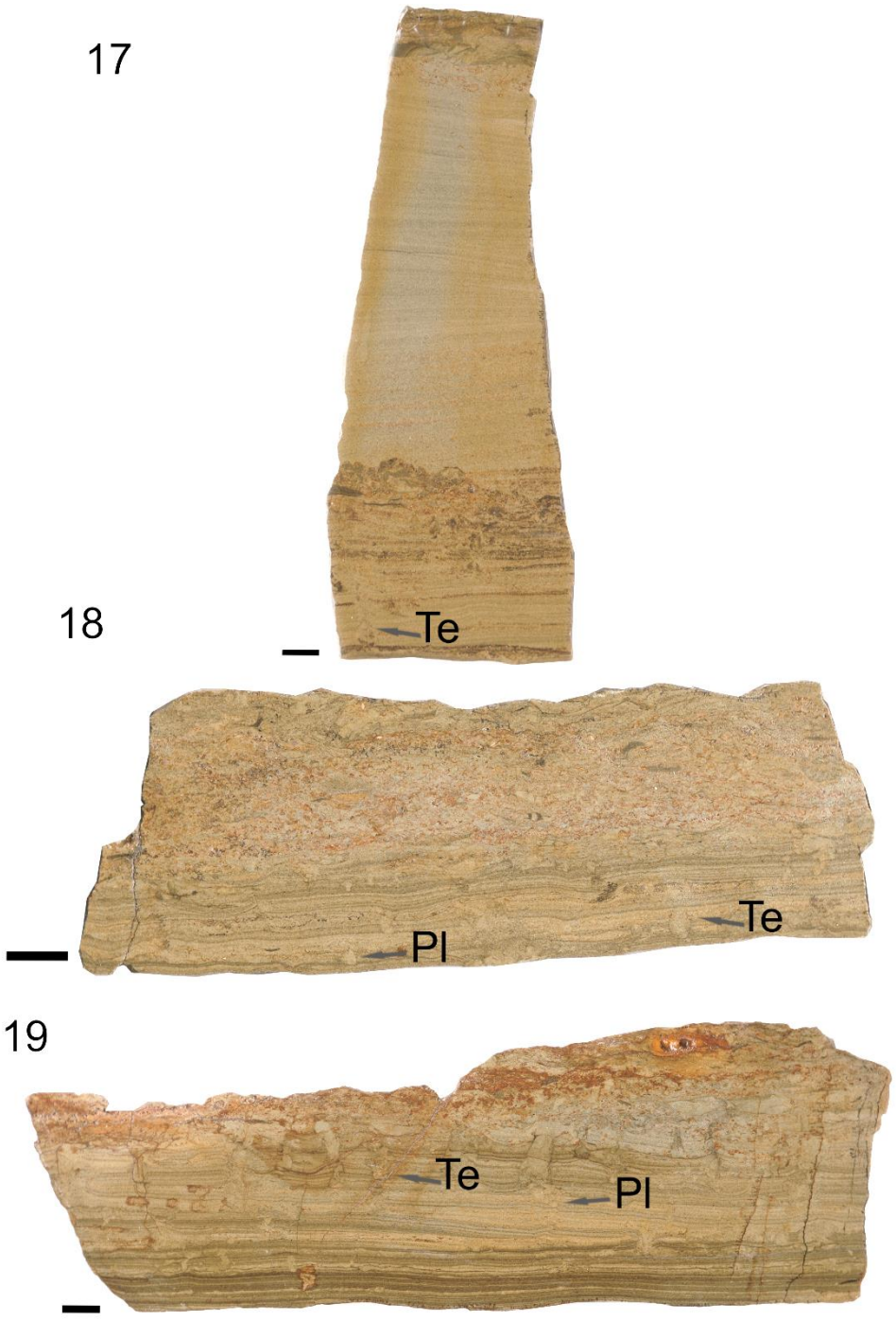
Cut sections of DBB at Weir quarry showing B.I., samples from collection points 14-16. The scale represents 1cm.

14) B.I. 3. Extensive bioturbation throughout the bed; good examples of *Teichichnus* sp. are seen in the lower part of the bed.

15) B.I. 1. No trace fossils present.

16) B.I. 1. No trace fossils present.

Plate 7.6



Explanation of Plate 7.6

Cut sections of DBB at Weir quarry showing B.I., samples from collection points 17-19. The scale represents 1cm.

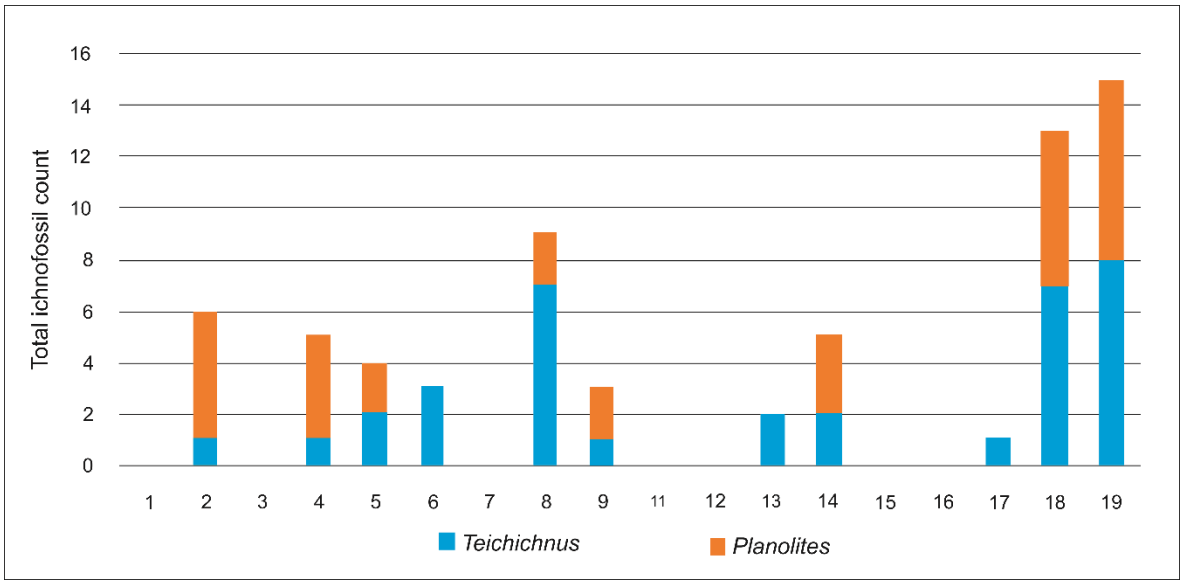
17) B.I. 2. There is slight bioturbation at the top of the bed, with only *Teichichnus* sp. being seen.

18) B.I. 4. The lower part of the bed shows examples of *Teichichnus* sp. and *Planolites* sp.

19) B.I. 4. The lower part of the bed shows examples of *Planolites* sp. while the upper shows many *Teichichnus* sp.

7.4 Diversity

The diversity of the trace fossils within the DBB at Weir Quarry is low with only two taxa present, *Teichichnus* sp. and *Planolites* sp. Despite this low diversity, they are numerous at specific points, such as sample points 18 and 19 (Text-fig. 7.5), suggesting the original patchiness in distribution and local variation in conditions.



Text figure 7.5 Graph of ichnofossil diversity and abundance across the section at Weir Quarry. Note that this records only identifiable ichnotaxa, so despite some points showing 0 trace fossils this does not mean that they are devoid of them.

7.5 Systematic ichnology

Family Incertae familiae

Genus TEICHICHNUS Seilacher, 1955

Type species: *Teichichnus* Seilacher, 1955, from the Lower Cambrian of the Salt Range, Pakistan

Teichichnus sp. Seilacher, 1955
Plate 7.1, Figure 2; Plate 7.2, Figure 4, 5 and 6; Plate 7.3, Figure 8 and 9; Plate 7.4, Figure 13; Plate 7.5, Figure 14; Plate 7.6, Figure 17, 18 and 19; Plate 7.7 Figure A and B; Plate 7.8, Figure A and B. Text Figure 7.6; Text Figure 7.7. Te.

Holotype: l e 1071/22, Palaeontological Collection, University of Tübingen, Germany.

Material: Thirty-three specimens found within horizon 1 and 3 of Bed 9 across the section at Weir Quarry.

Diagnosis (after Knaust 2018): Vertical to oblique, unbranched or branched, elongated to arcuate spreite burrow with stacked convex-down and/or convex-up laminae and a passively filled terminal causative burrow. Funnel-like extension of the tube and wall ornamentation may be present.

Description: Elongate vertical burrows 15-27 mm long, 1-10 mm wide. The walls of the traces are picked out by darker sediment, and the infill is a lighter colour (a pale tan) than the host rock (Text-fig. 7.6). Spreiten structures are present within some of the traces. The grain size of the infill of the burrows is larger than the matrix: there is generally a higher proportion of quartz grains and less clay (Text-fig. 7.7).

Remarks: *Teichichnus* is considered to be an example of fodinichnia (Seilacher 2007), where the trace maker is foraging for food. Various organisms have been suggested as the trace maker, as *Teichichnus* is known across the Phanerozoic; possible trace makers are annelid worm and arthropods.

Genus PLANOLITES Nicholson, 1872

Planolites sp.

Plate 7.1, Figure 2; Plate 7.2, Figure 4 and 5; Plate 7.3, Figure 8 and 9; Plate 7.6, Figure 18 and 19; Plate 7.7 Figure B; Plate 7.8, Figure A; Text Figure 7.6; Text Figure 7.7. Pl.

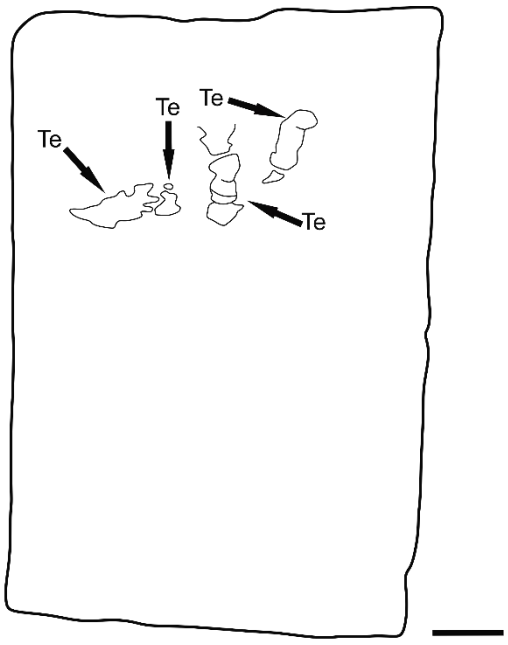
Material: Thirty-two specimens found within horizon 1 and 3 of Bed 9 across the section at Weir Quarry.

Description: Cylindrical horizontal or low-angle burrows with an oval cross-section preserved in full relief ranging in width from 1 mm to 7 mm. The traces are picked out in the same way as *T. rectus* (Text-fig. 7.6). In thin section the traces exhibit the same preservation as *Teichichnus*, marked by a higher percentage of quartz to clay. Another feature, only clearly seen in thin section (Text-fig. 7.7), is that many burrows are deformed from their original round shape and have irregular boundaries.

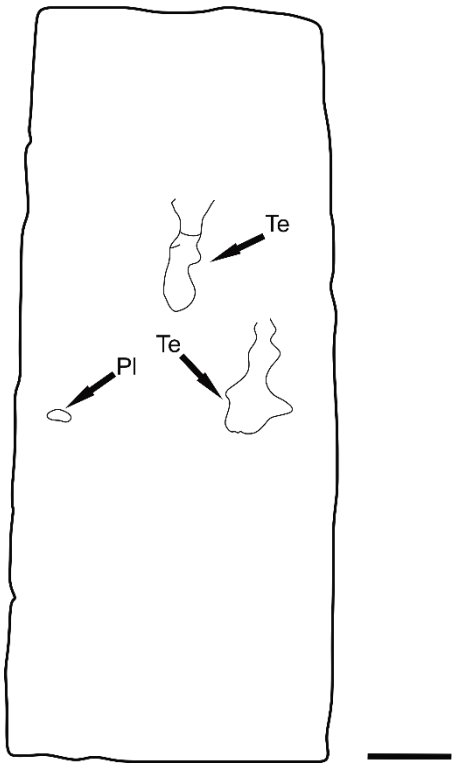
Text figure 7.6 Cross-section of Downton Bone Bed showing both trace fossil taxa present within the bed; Te is *Teichichnus* sp. Pl is *Planolites* sp.; scale represents 1 cm.

Plate 7.7

A



B



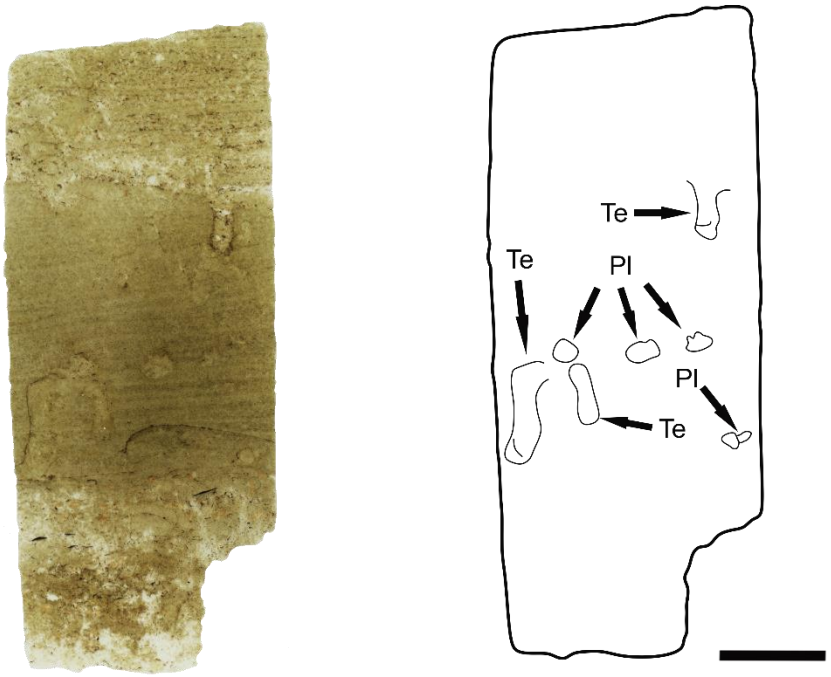
Explanation of Plate 7.7

A) Thin section of DBBI15 with traces present in horizon 3; all traces are *Teichichnus* sp. (Te). The scale represents 1 cm.

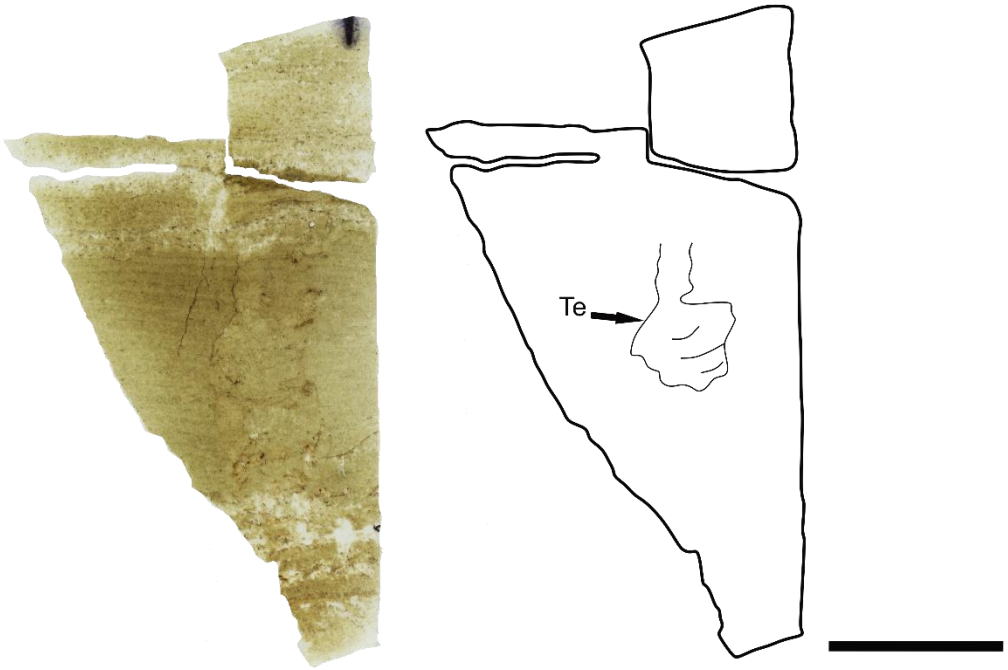
B) Thin section of DBBI13 with traces present in horizon 3; traces are *Teichichnus* sp. (Te) and *Planolites* sp. (Pl). The scale represents 1 cm.

Plate 7.8

A



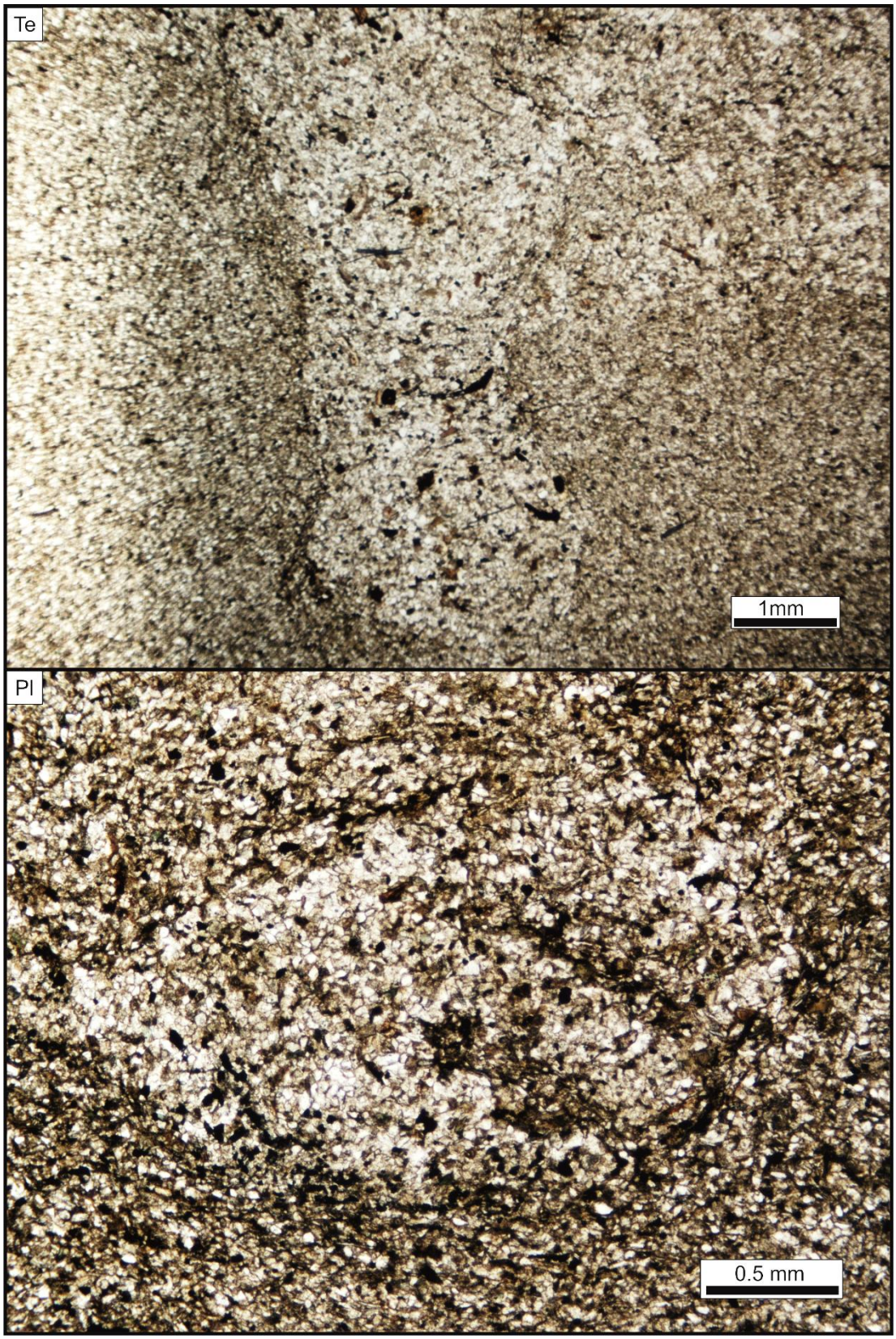
B



Explanation of Plate 7.8

A) Thin section of DBBI12 with traces present in horizon 3; traces are *Teichichnus* sp. (Te) and *Planolites* sp. (Pl). The scale represents 1 cm.

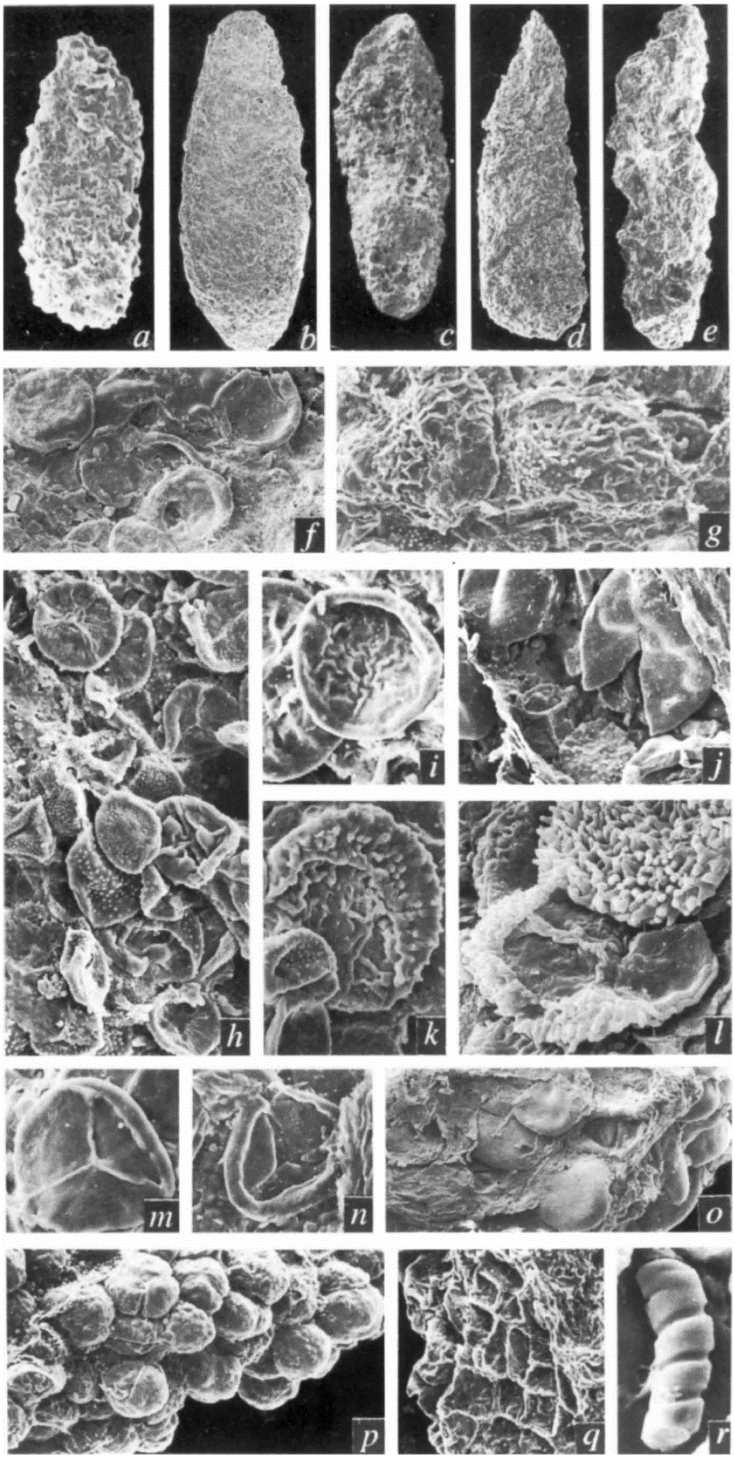
B) Thin section of DBBI14 with traces present in horizon 3; all traces are *Teichichnus* sp. (Te). The scale represents 1 cm.



Text Figure 7.7 Thin sections of the trace fossils in the Downton Bone Bed in PPL; Te is *Teichichnus* sp., and Pl is *Planolites* sp.

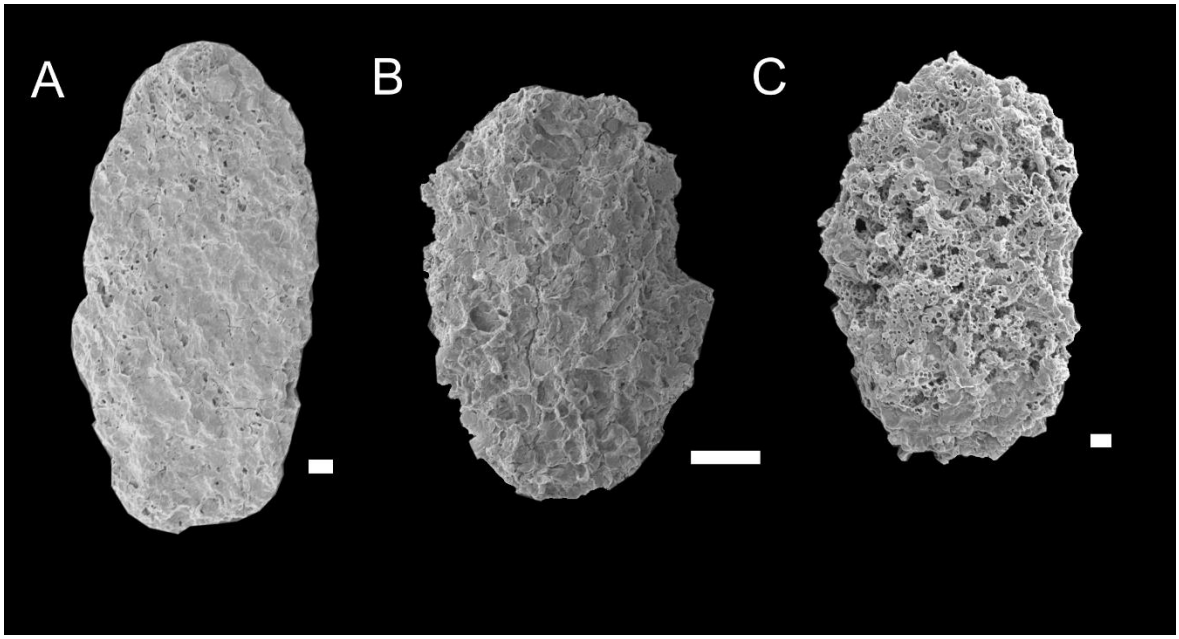
7.5.1 Coprolites

Within the organic residues of the DBB were found what appeared to be several isolated sporangia. However, their morphology was reminiscent of the material described in Edwards et al. (1995) as coprolites (Text-fig 7.8).



Text figure 7.8 Edwards et al. (1995) fig. 1 a-e show similar morphology and structure to the material from the DBB at Weir Quarry (Text-fig 7.9).

Other features were also noticed, such as the apparent mix of spores within a single specimen, and that some spores appeared damaged, which was not seen in other sporangia. Through discussion with Prof Edwards (pers. comm. 2019) is was clear that unless the specimens were broken open, it could not be determined for certain if they were coprolites, although these three specimens are likely to be coprolites (Edwards pers. comm. 2019).



Text figure 7.9 Three possible coprolites from the Downton Bone Bed at Weir Quarry A) DBB2.53.1 B) DBB14.53.C) DBB4.53.3.

7.6 Discussion

7.6.1 Infaunal trace fossils

The previous chapters discussing the fossil content of the DBB at Weir Quarry have all pointed out that the overall diversity of fossil organisms within the DBB appears to be low. This is also the case for the trace fossils although the upper part of the bed (horizon 4) is often heavily bioturbated. The horizons associated with the background conditions before the "bone"-rich layers of the DBB were laid down (horizons 1 and 3) which usually show the planar/quasi-planar laminations are only populated with two trace fossils *Planolites* and *Teichichnus.* This is not a diagnostic assemblage. As is often the case with ichnofacies communities there are multiple key ichnogenera present allowing for an interpretation of the depositional setting the traces formed in (Knaust 2017). However, there are two environmental settings where the presence of only *Planolites* and *Teichichnus* can be diagnostic. Buatois and Mángano (2011) described how *Planolites* and *Teichichnus* are the most common trace fossils in severely restricted settings, and one feature of these environments is that they are characterized by fluctuating salinity, this is supported by the presents of syneresis cracks (Text-fig 3.22). MacEachern and Gingras (2006) described the key characteristics of the brackish-water trace-fossil suites of the Grand Rapids Formation, the Weseca Formation and the Paddy Member of the Cretaceous of Alberta, Canada. They stated that *Planolites* and *Teichichnus* can be diagnostic of dysaerobic (a depositional environment with 0.1–1.0 ml of dissolved oxygen per litre of water) conditions. These two traces then suggest that the environment where the traces were made was a low oxygen setting with a fluctuating salinity resulting in a low diversity of trace fossils. Caution should be taken however with this being a direct interpretation, as the colonisation of brackish water sediments from different ichnofauna have changed over geologic time (Buatois et al. 2005).

7.6.2 Coprolites within the Downton Bone Bed

The specimens from the DBB at Weir Quarry (Text-fig. 7.9) are very similar to the material figured in Edwards et al. (1995). Edwards et al. (1995) discussed the identity of the trace maker. The first point is to establish is whether these coprolites were produced by terrestrial or aquatic invertebrates. The dominant preserved aquatic animals during the late Silurian were the eurypterids (Brett and Walker 2002). Many

of them lived in marginal marine environments (Selden 1984). Evidence pointing to a terrestrial origin comes from the coprolites being composed of terrestrially derived spores. They also are preserved in the same manner as the terrestrial plant fossils within the bed. The next question is, were the animals herbivores or detritivores? Herbivory is a specialized feeding method that usually requires the aid of fungi or gut bacteria to aid in digestion (Southwood 1985). However, spores and sporangia are energy-rich and high in nitrogen (Demmaggio and Stetler 1980; Mattson 1980). It has been suggested that spore feeding may have preceded herbivory in invertebrate evolution (Edwards et al. 1995). In the material studied by Edwards et al. (1995) they suggested that the animals were feeding on spores and immature sporangia. Extant pollen feeders obtain nutrients either by mechanical lysis (beetles) or chemical means (such as enzyme secretion in modern flies). Mechanical lysis seems unlikely as both the Edwards et al. (1995) specimens and the material from the DBB are nearly all complete. If herbivory is not a viable mode of feeding for the trace maker, then perhaps the coprolites were produced by detritivores. Detritivores feed on litter; it seems likely that if these coprolites do belong to detritivores, then they were feeding on spores and spore masses. This is seen in the specimens figured by Edwards et al. (1995), who suggested that this would account for the spore diversity within a single coprolite. If the animals were selectively feeding or were coprophagous, this would account for the high spore concentration (Edwards et al. 1995). The detritivore hypothesis would also explain the lack of bacteria and fungi seen in the DBB samples and samples studied by Edwards et al. (1995, 2012), and Hagström and Mehlqvist (2012). It seems likely then that the coprolites seen in the DBB at Weir Quarry, which are very similar to those figured by Edwards et al. (1995), were produced by a detritivore, potentially a millipede or one of its kin (Shear et al. 2001).

8. A review of Silurian bonebeds

8.1 Introduction

The definition of bonebeds has been discussed in detail (Chapter 1, section 1.2 which should be referred to for further information). This chapter will review and discuss the known bonebeds from the Silurian (according to Rogers et al. 2007).

8.1.1 Previous work

The first formally recognised Silurian bonebed was by Sir Roderick Impey Murchison in the *Silurian System* in which he described the Ludlow Fish Bed (Murchison 1839) which he later (1853) renamed the Ludlow Bone Bed. The LBB and the other Early Palaeozoic bonebeds differ from later Phanerozoic bone beds in that they contain very little actual bone. The vast majority of the Early Palaeozoic vertebrates possessed a cartilaginous endoskeleton, and their skin was covered in a squamation of denticles which are more similar to teeth than to bone in their histology. So, as the dominant vertebrates of the DBB, the thelodonts, did not have true bone, perhaps the term 'tooth bed' would be more accurate! In this review of the known "bone beds" from the Silurian, there is a maximum of five confirmed bonebeds located in only two countries (Text-fig. 8.1). All of the bonebeds discussed in this chapter are classified as multitaxic bonebeds as defined in Chapter 1. Taxa recorded from the various bonebeds are listed in Table 8.1.

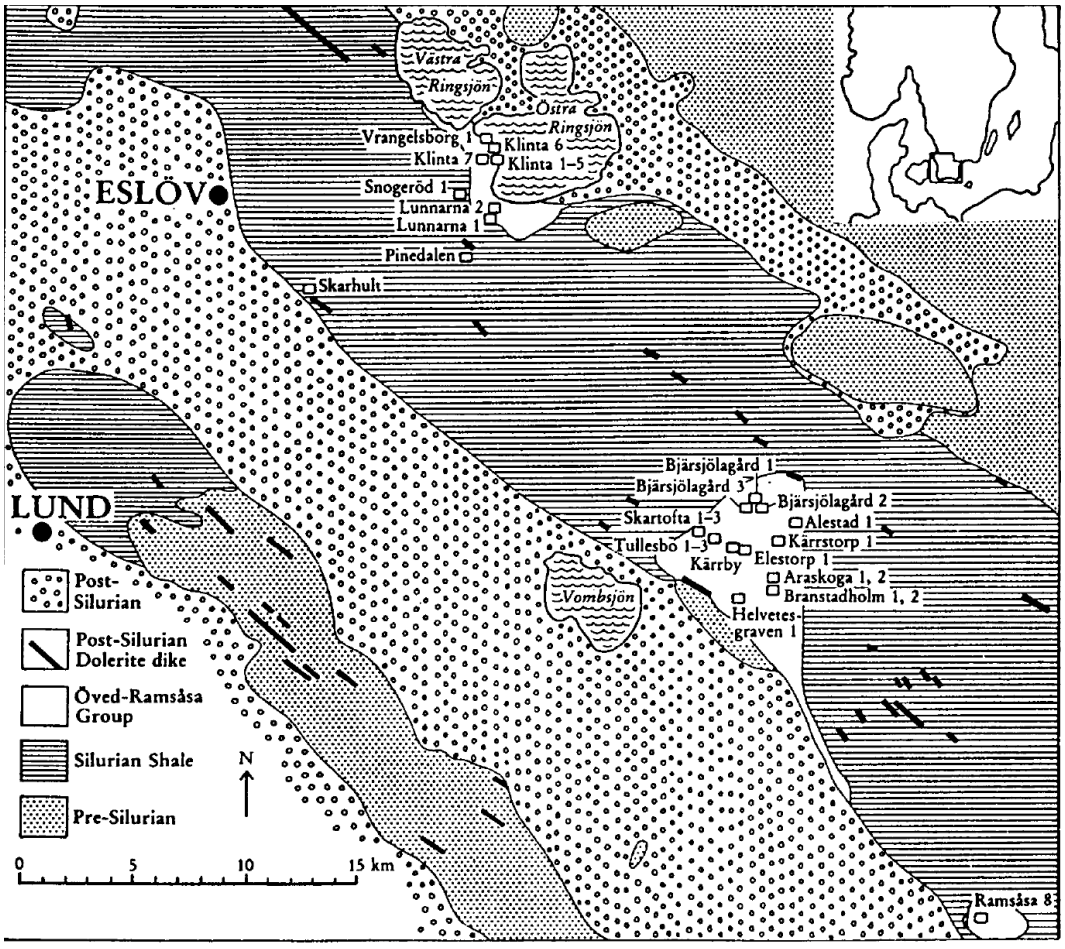
Taxon	Bone Bed			
	Southern Sweden	Ludlow	Temeside	Downton
Agnatha				
Osteostraci				
Hemicyclaspis murchisoni		X	X	X
Hemicyclaspis lightbodyii			X	
Hemicyclaspis sp.				X
cf. *Hemicyclaspis*	X			
Sclerodus pustuliferus		X		X
Auchenaspis salteri			X	
Thelodonti				
Thelodus parvidens	X	X		X
Thelodus traquairi	X			
Thelodus costatus				
Thelodus admirabilis	X			
Thelodus sculptilis	X			
Thelodus biocostatus		X		
Thelodus pugniformis		X		
Thelodus trilobatus		X		
Loganellia cuneata	X			
Paralogania ludlowiensis		X		X
Gnathostomata				
Acanthodii				
acanthodians indet.				X
Nostolepis striata	X			
Gomphochus sp.		X		X
Gomphonchus sandelensis	X			
Plectrodus mirabilis		X	X	
Plectrodus sp.			X	
Plectrodus peliopristis		X		
Onchus murchisoni		X	X	X
Onchus tenuistriatus		X		
Actinopterygii				
Andreolepis hedei	X			

Table 8.1 List of taxa found in the multitaxic Silurian bone beds. Data taken from Vergoossen (1999) and Dineley and Metcalf (1999).

Text figure 8.1 World map identifying the position of confirmed Silurian bonebeds, CF refers to the Caledonian Front, IS refers to Iapetus suture and TS to the Thor suture (Modified from Torsvik and Cocks 2016).

8.2 Silurian bone beds in Southern Sweden

The bone beds of southern Sweden (Text-fig. 8.2) have been known since the mid-20th century with Lehman (1937) first describing the vertebrate remains from the Helvetesgraven Quarry, which went out of use in the 18th century and is now flooded. The quarry exposed parts of the Öved Sandstone Formation, Öved-Ramsåsa Group, with two sections available both showing a reddish sandstone (Jeppsson and Laufeld 1986; Vergoossen 1999b). The Öved Sandstone contains sandstones, shales and subordinate thin limestone bands showing marine faunas with the increased abundance of bivalves higher in the section suggesting a shallowing-upward trend (Jeppsson and Laufeld 1986; Vergoossen 1999b). Vergoossen (1999b) studied material (Osteostraci, Theleodonti, Acanthodii and Osteichthyes) that had been collected by Stensiö in 1924 and was held in the Palaeozoology Department of the Swedish Museum of Natural History, Stockholm.



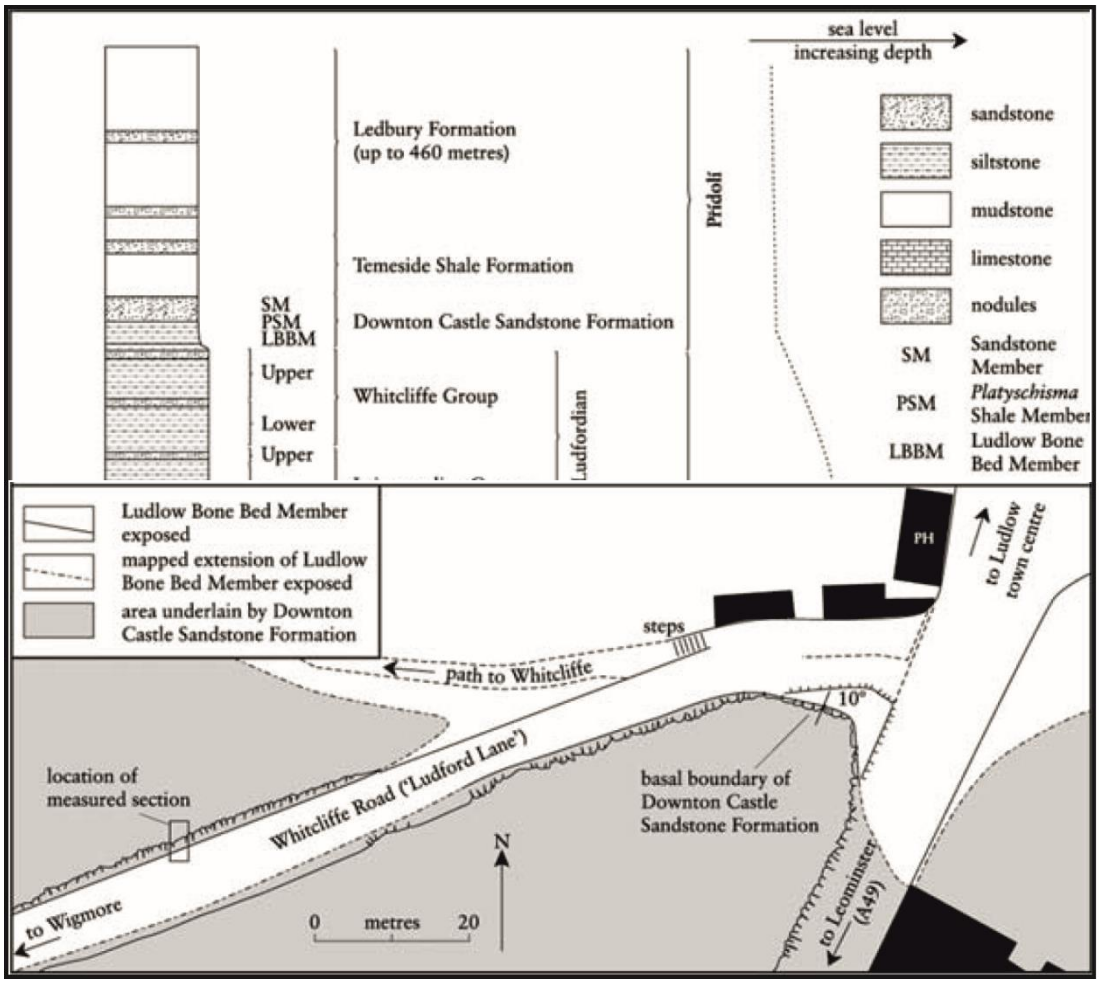
Text figure 8.2 Map of Skåne, indicating the location of the Helvetesgraven Quarry (taken from Vergoossen 1999).

It is thought that the samples, collected from dump piles, could be parts of the same 10-20 mm thick dark red lens, with one side being mottled with cm-sized red clasts on a grey surface and which has mm-sized white fossil fragments presumed to be conodont and fish fragments by Jeppsson and Laufeld (1986). The latter authors also noted that the samples were slightly calcareous and broke down very slowly in acetic acid.

There is very little direct information on the palaeoenvironment at Helvetesgraven; however, Wigforss-Lange (2007) studied the tidal facies in the upper Silurian Öved-Ramsåsa Group including a locality at Klinta which is *c.*17 km north from the Helvetesgraven 1 locality studied by Vergoossen (1999b). Wigforss-Lange used evidence from the sedimentary structures, rapid vertical changes in lithologies and the lateral variability of beds to suggest that the sequence represents a regressive marine succession, indicative of tide-dominated sedimentation in a shallow epeiric sea. The age of the Öved Sandstone is Přídolí based on conodonts (Vergoossen 1999b), but Vergoossen also recorded the occurrence of three key taxa (Table 8.1) *Andreolepis hedei*, *Thelodus sculptilis*, *T. admirabilis*, that suggested a different, earlier date within the late Silurian. Märss (1992) suggested that the co-occurrence of these taxa is typical of the short duration *A. hedei* event which marks the transition between the *hedei* and *sculptilis* biozones of the Silurian Vertebrate Standard Zonation (Märss 1992). The event falls within the *snajdri* Conodont Interval Zone of the upper Ludfordian (Märss et al. 1995). The crucial thelodont biostratigraphically is *T. admirabilis*, which is known from the Tahula Beds on the western slopes of the Central Urals, Kuressaare Regional Stage, Ludfordian (Vergoossen 1999b). *T. admirabilis* outnumbered *T. sculptilis* in Vergoossen's picked samples by 2:1 suggesting a younger age to Vergoossen of the Laurussian faunas that were affected by the *hedei* Event (due to the greater abundance of *T. admirabilis* than in any of the faunas affected by the *hedei* Event). Finally, the presence of *Hemicyclaspis*-like scales links the Helvetesgraven fauna to the Burgsvik Sandstone of Gotland, which is again dated to the Ludfordian (Vergoossen 1999b). In conclusion, Vergoossen (1999b) considered there to be two bonebeds at Helvetesgraven: a lower bonebed of late Ludfordian age and an upper bonebed within the upper Přídolí. As Vergoossen did not give formal names to these bonebeds, it is suggested that they are referred to from this point on as the Lower and Upper Helvetesgraven Bone Beds.

8.3 The Ludlow Bone Bed, England and Wales

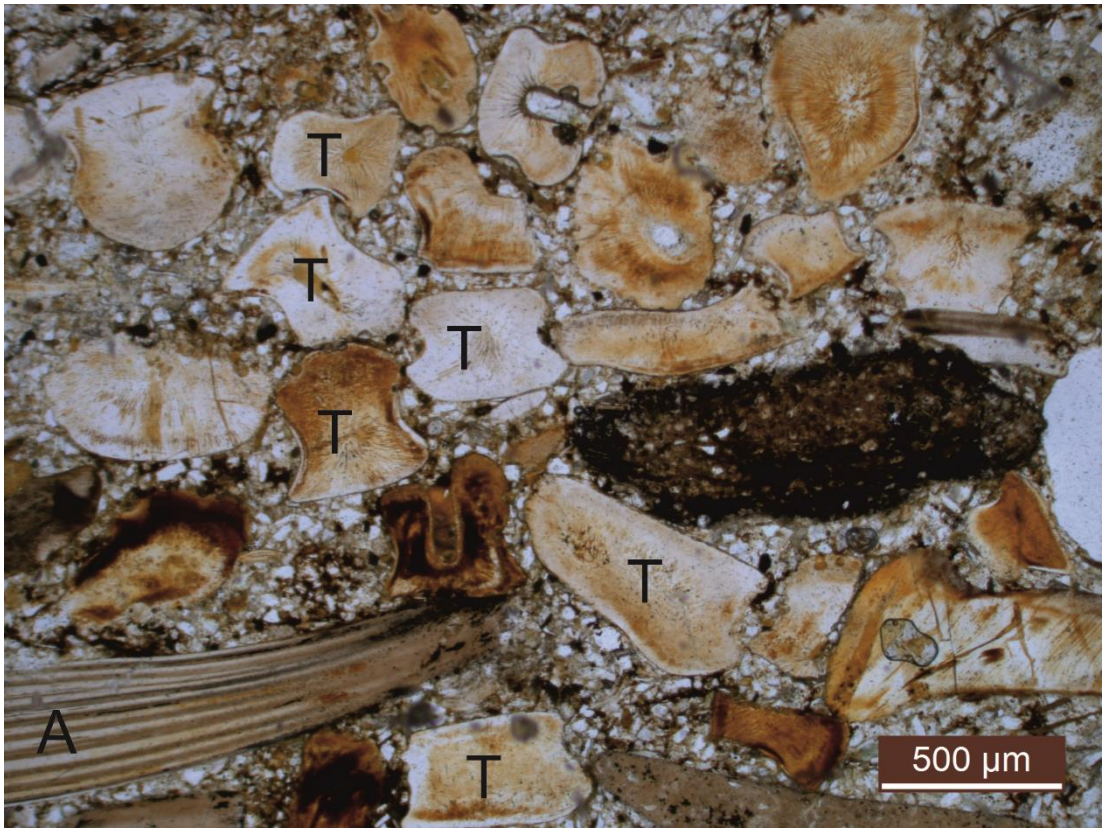
This is the best known of the Silurian bonebeds and was the first recorded (Murchison 1839) after being found by Dr J. Lloyd and the Reverend T.T. Lewis in 1835, at Ludford Corner in Ludlow, Shropshire, U.K. (Text-fig. 8.3). It is found stratigraphically at the base of the Downton Castle Sandstone Formation and forms the lowermost member, the Ludlow Bone Bed Member (LBBM) (Bassett et al. 1982). The fish fossils found within the bonebed were described by Agassiz (1839) and for a considerable length of time represented the earliest fish in the fossil record (Symonds 1872; Lapworth 1879; Stamp 1923). During the mid-20th century, the base of the LBBM was considered to mark the base of the Devonian (White 1950), although this was due to a mistranslation of Murchison by Darlodot (1912) and later marked the base of the upper Silurian Downton Series (Holland et al. 1963; Bassett et al. 1982). Subsequent to the original 1839 description, the LBB has received a great deal of attention (Murchison 1853, 1867; White 1950; Whitaker 1962; Holland et al. 1963; Turner 1973; Antia and Whitaker 1979; Antia 1979a, 1979b, 1980; Bassett et al. 1982; Siveter et al. 1989; Smith and Ainsworth 1989; Märss and Miller 2004). It was demonstrated that the age of the LBB is mid-Ludfordian (late Ludlow) using $\delta^{13}C_{org}$ data to correlate the CIE (carbon isotope excursion) associated with the Lau event (Loydell and Frýda 2011). It was stated by Loydell and Frýda (2011) that "with the exception of the presence of the ostracod *Frostiella groenvalliana* in the Ludlow Bone Bed Member, all data (conodont, thelodont, lithological, sequence stratigraphical and carbon isotopic) are consistent with the Ludlow Bone Bed Member being of mid Ludfordian age." There has been no evidence since to suggest that the dating of the LBB by Loydell and Frýda (2011) is incorrect, although some authors (e.g. Kaljo et al. 2015) require further analysis of the UWF before it accepted with certainty regarding the mid Ludfordian attribution.



Text figure 8.3 Stratigraphy of the Ludlow area and map of the Ludford lane locality (modified from Dineley and Metcalf 1999).

The lithology of the LBB is a coarse sandstone which is interbedded with ripple laminated lenticular bedded siltstones. The LBBM also contains additional thin bone-bearing horizons, which lie above the main bonebed (Antia 1979a, 1979b, 1980). The LBB has been suggested to be a lag deposit formed in shallow subtidal to low intertidal conditions (Dineley and Metcalf 1999). The distinctive "gingerbread" appearance (Murchison 1839) of the LBB is due in part to it being formed during a marine regression with a low sedimentation rate which allowed the deposit to be winnowed (Dineley 1951). The LBB represents the first marker of this marine regression in the Welsh Borders, which would eventually lead to the Old Red Sandstone facies in Britain (Dineley and Metcalf 1999). The vertebrates within the LBB (Table 8.1) (Text-fig. 8.4) have been intensively studied (Agassiz 1839; M'Coy 1853; Harley 1861; Marston 1882; Woodward 1891, 1904; Woodward and Dixon

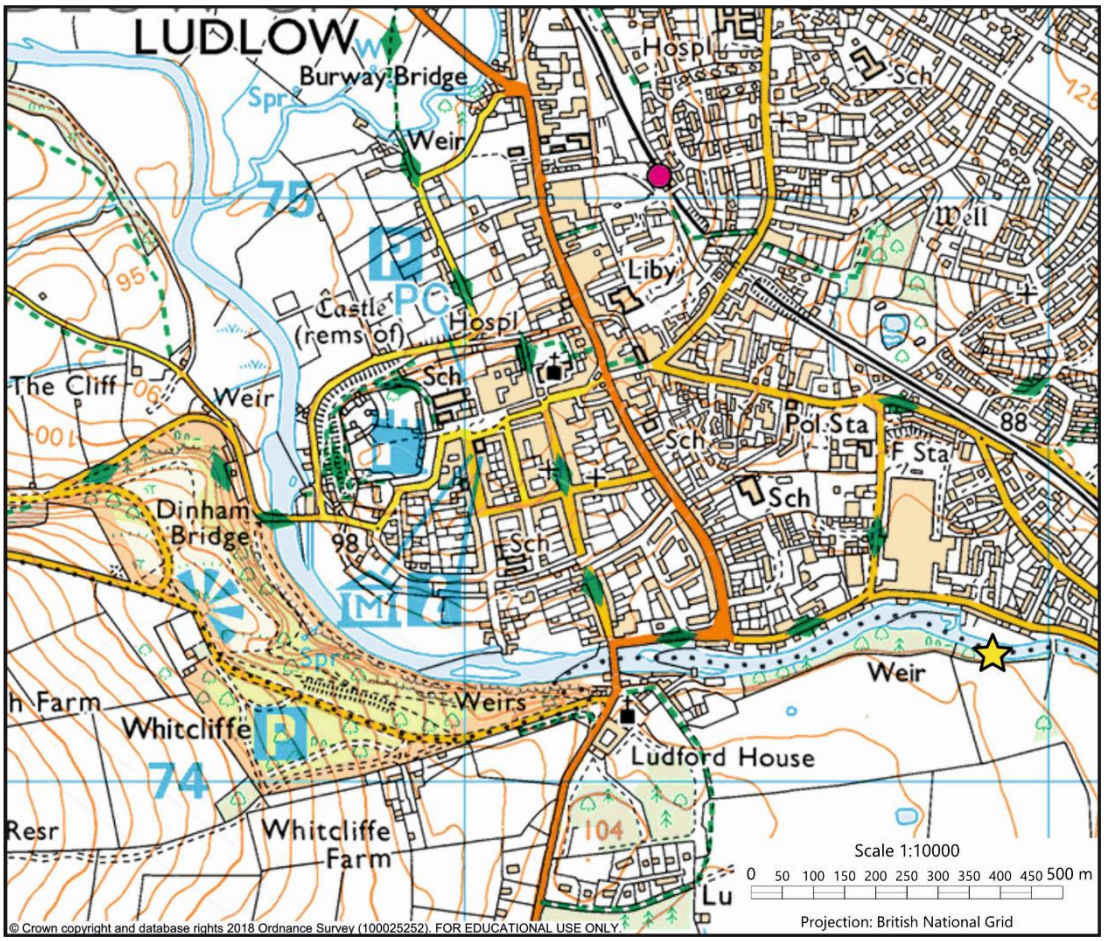
1904; Lankester and Traquair 1914; Gross 1957, 1967; Denison, 1956, 1974, 1979; Turner 1973, 1976; Forey 1987; Dineley and Metcalf 1999; Märss and Miller 2004).



Text figure 8.4 Thin section of Ludlow Bone Bed in PPL with thelodont denticles (T) and acanthodian fin spine (A).

8.4 The Temeside Bone Bed, England and Wales

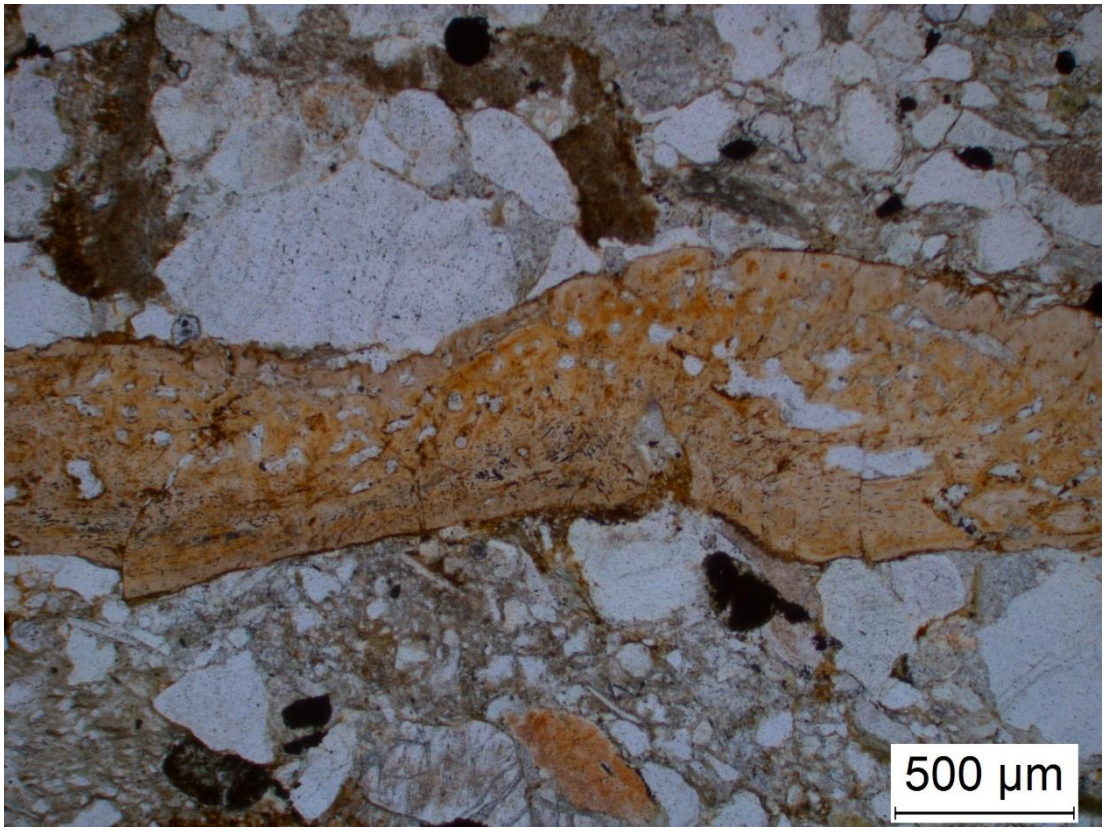
The stratigraphically highest bonebed in the Welsh borders late Silurian succession was first recorded by Murchison (1856) and later named by Elles and Slater (1906) on the right bank of the River Teme in Ludlow (Text-fig. 8.5) (Dineley and Metcalf 1999). It is within the Temeside Shale Formation which succeeds the DCSF. It was described in detail by Antia (1981) who remarked on the presence of clayey sub-bone-bed infilling scour hollows on the surface of the calcrete crust of the red beds. He added that the presence of mud balls, highly abraded and weathered fish scales, comminuted shell fragments and algal plant debris pointed to a depositional site within the supratidal zone, noting that these types of deposits often mark the onset of a marine regression.



Text figure 8.5 Map indicating the locality (yellow star) of the Temeside bonebed first recorded by Murchison (Image taken from Digimap 2018, grid reference SO 520 742 taken from Antia 1981).

The fossils of the bed have been published upon frequently over the last 160 years (Murchison 1853; Egerton 1857; Roberts 1865; Lankester 1870; Woodward 1891; Kiaer 1931; Stensiö 1932; Gross 1947; White 1950; Whitaker 1962; Allen and Tarlo 1963; Antia 1981; Janvier et al. 1985; Dineley and Metcalf 1999). The lithology of the TBB is a coarse sandstone often referred to as a ‘grit’ (e.g. Egerton 1857; Elles and Slater 1906), which is both underlain and overlain by a fine-grained olive green silt/sandstone, that weathers with the same oxidised surface colour that is seen in the DBB. Elles and Slater (1906) described it as being more ‘diffuse’ than the LBB, and this is the case with samples examined from the Sedgewick Museum of Earth Sciences collection (Text-fig. 8.6). The samples examined appeared to have less vertebrate material overall than the DBB samples from Weir Quarry (although its vertebrate material was larger in overall size). Pieces of agnathan (Thelodonti and Osteostraci) and gnathostomes (Acanthodii) and coprolites have been recorded from the TBB (Table 8.1).

Further sedimentological work using thin sections would be useful to describe the lithology in detail as well, enabling the description of the nature of the contact between the fine and coarse beds. A palaeoenvironmental interpretation for the TBB was presented by Antia (1981), who suggested that it represents a channel lag deposited in a back beach/lagoonal mud during a gradual marine regression. The age of the Temeside Shale Formation is stated to be Přídolí by Miller and Märss (1999), referring to the work of Gross (1967), Turner (1973) and Antia (1979) as shown in Miller and Märss text-fig 1_A (p. 692).



Text figure 8.6 Temeside Bone Bed in PPL with a large piece of Osteostraci running across the micrograph.

8.5 Discussion

8.5.1 Silurian bonebeds

The bonebeds that have been reviewed within this chapter are summarised in Table 8.2. They all formed towards the end of the Silurian, and this probably reflects the global trend of regressions taking place throughout the late Silurian (Haq and Schutter 2008). This would also account for the commonality in shallow marine depositional environments.

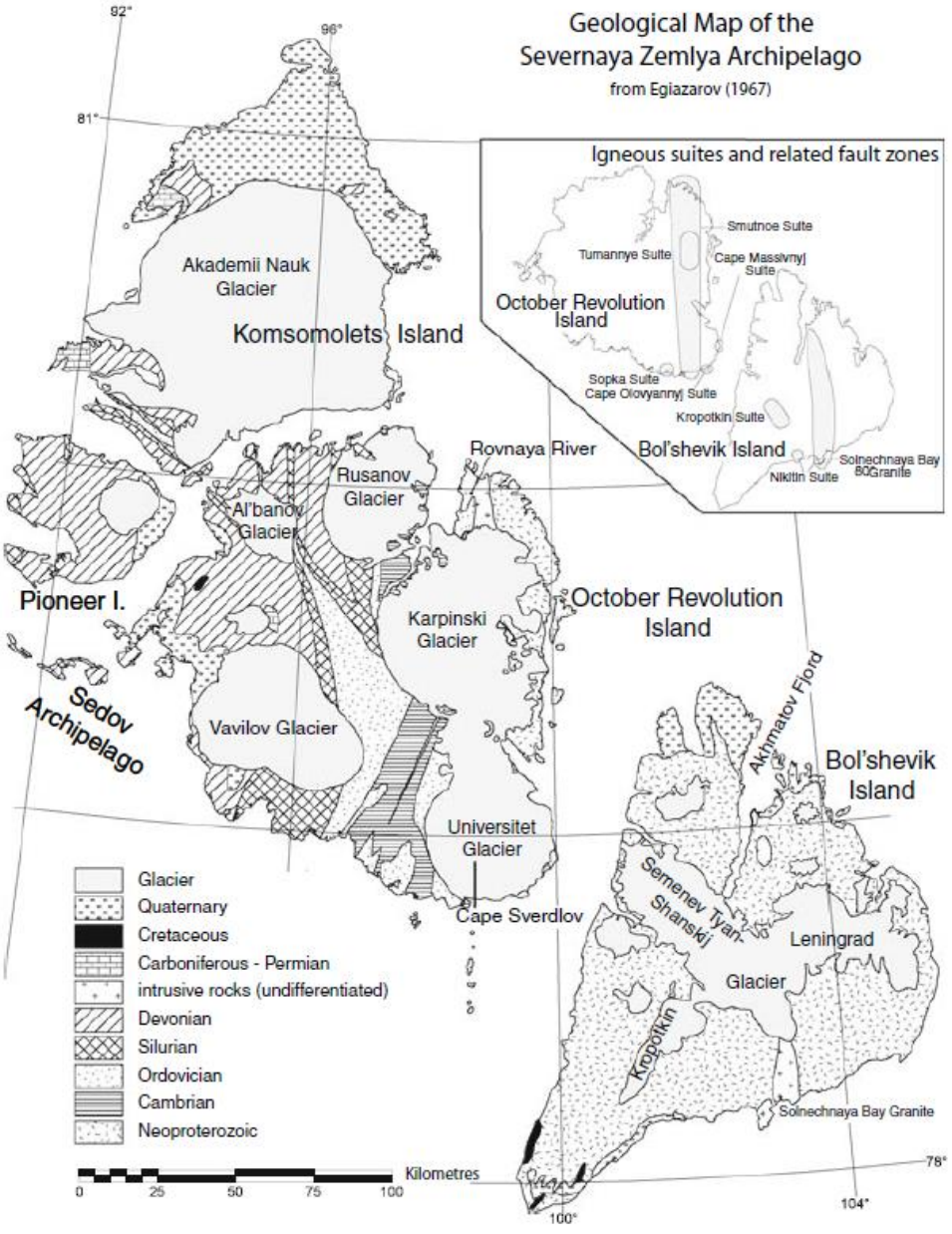
Name	Country	Epoch/Age	Depositional environment
Ludlow Bone Bed	England	Ludlow/ Ludfordian	Marine; intertidal; back barrier
Temeside Bone Bed	England	Ludlow/ Ludfordian	Marine; intertidal; back barrier
Upper Swedish Bone Bed	Sweden	Přídolí	subtidal/intertidal lagoon or sheltered embayment
Lower Swedish Bone Bed	Sweden	Late Ludfordian	subtidal/intertidal lagoon or sheltered embayment

Table 8.2 Summary of Silurian bonebeds reviewed in this chapter.

The bonebeds reviewed here are only the ones that were regarded by Rogers et al. (2007) to be classified as bonebeds; however, there are other vertebrate deposits from the Silurian in other parts of the world. An example is the Osel Bone Bed from the island of Osel, Estonia. This was discussed in detail by Antia (1979b). However, some workers who have studied the Silurian vertebrates of Estonia for decades do not regard the Osel deposit that Antia described as a bonebed (Märss pers comm. 2016). This disagreement is symptomatic of the lack of clarity in defining what a bonebed is or is not. Further study and a research consensus are required to consider if these outliers should also be regarded as bonebeds. There are other locations that are known to be rich in vertebrate material, but they are not described as coming from bonebed deposits. These localities include Arisaig, Canada, the Severnaya Zemlya Archipelago, Russia, multiple sites across Australia and Yunnan, Southwestern China.

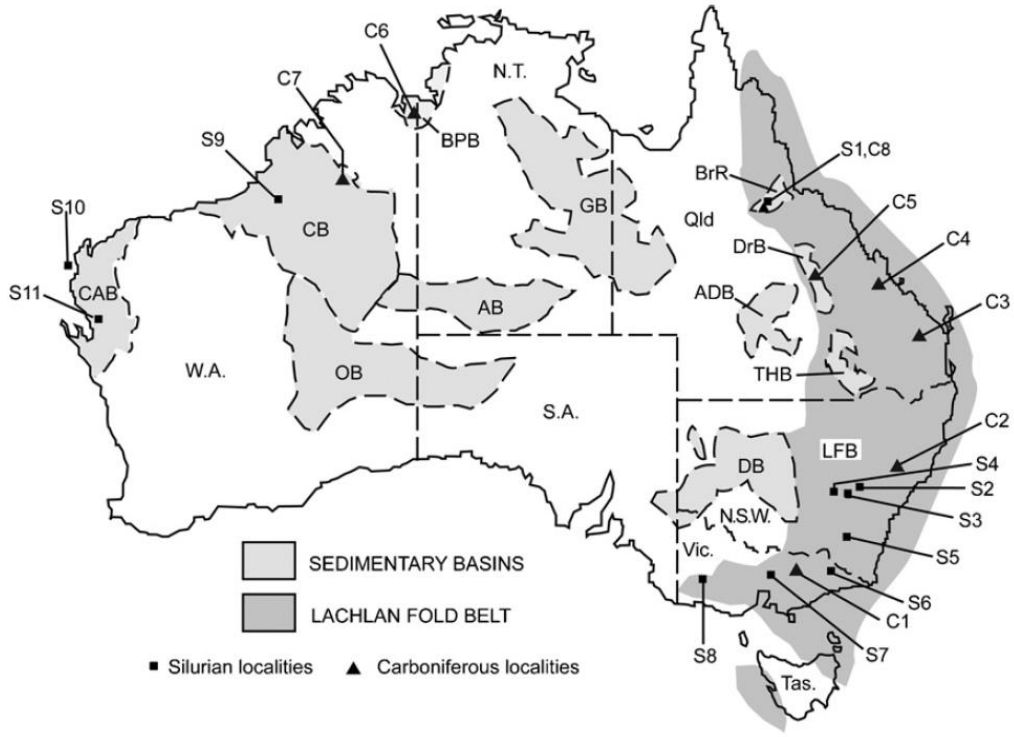
Arisaig, Nova Scotia, Canada has previously been discussed in Chapter 4, so in brief, it is a vertebrate bearing deposit from the upper Silurian that shares a similar faunal diversity with the DBB and the other Welsh Borders bonebeds; however, it is not recorded as a locality that contains bonebeds (Burrow et al. 2013).

The Severnaya Zemlya Archipelago, Russia, has yielded various thelodont denticles from across the duration of the Silurian, but all are described as being isolated (Karatajūtē-Talimaa and Märss 2002). Although there are significant outcrops of Silurian strata (Text-fig. 8.7) there are no bonebeds recorded within the Silurian.



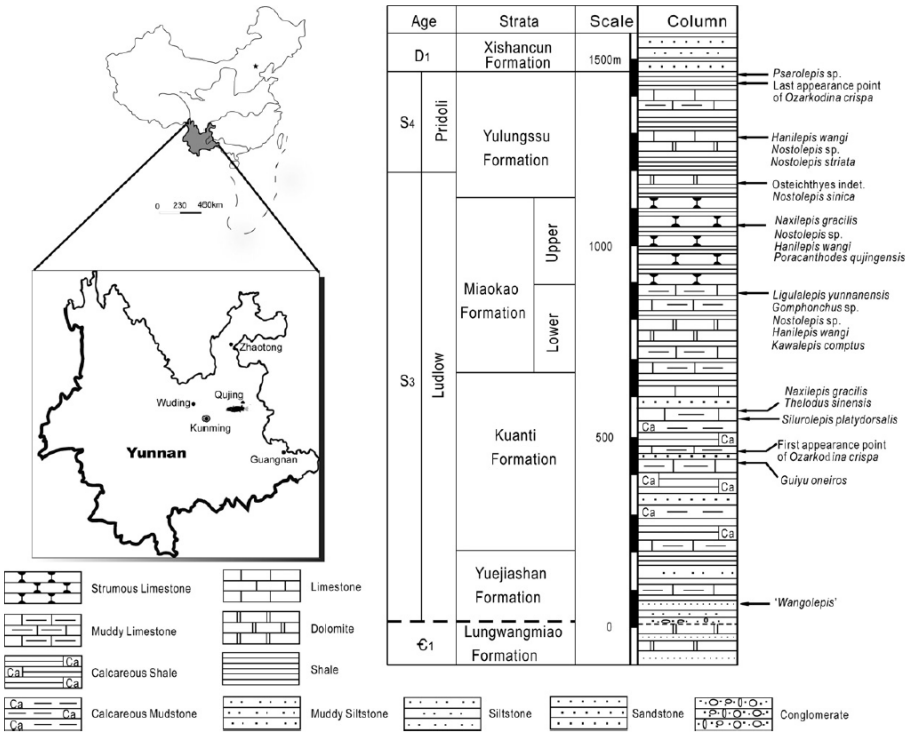
Text figure 8.7 Geological map of Severnaya Zemlya Archipelago (taken from Lorenz et al. 2008).

Australia is a continent that is rich in Silurian and other Palaeozoic vertebrates and micro-vertebrates (Text-fig. 8.8), but no deposits from the literature are described as bone beds (Burrow et al. 2010). The reason may be simply that throughout and particularly in the upper Silurian of Australia, the conditions needed to form bonebeds were not present. Another possible consideration is that a sample recently described was obtained from a drill-core (Burrow et al. 2019). One issue with core samples is it is harder to appreciate the broader context of a sample, for example is it only a localised lens of material or is it a continuous bed?



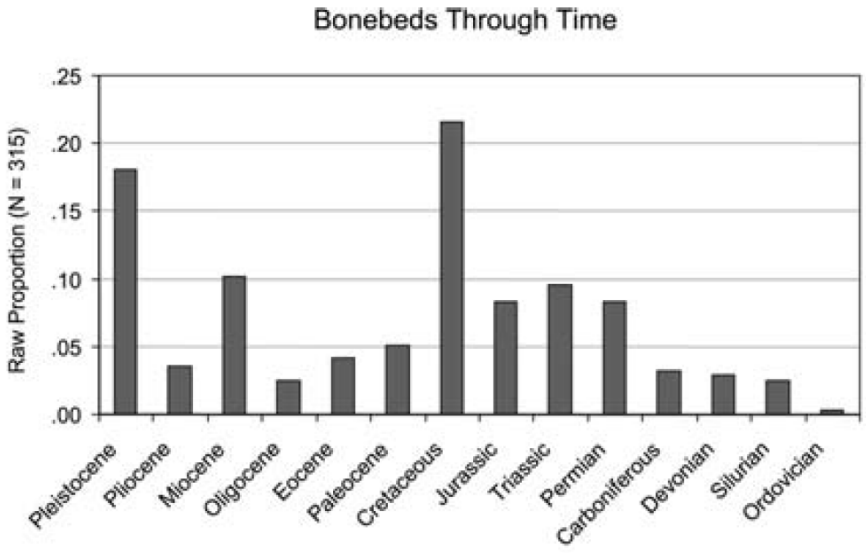
Text figure 8.8 Map of Australia showing all of the Silurian localities (square symbol) and S-numbers (i.e. S1) (taken from Burrow et al. 2010).

Yunnan Province, Southwestern China is famous for the Xiaoxiang fish fauna. This contains taxa such as *Guiyu oneiros* and *Megamastax amblyodus* (Text-fig. 8.9). These vertebrates are particularly well preserved (Cui et al. 2019) having been deposited in a marine embayment (Fang et al. 1985; Zhu and Zhao 2009), however due to the taphonomy of the specimens and the size of the vertebrate material (Choo et al. 2014) it would suggest that there was a low energy regime that was not conducive to the formation of bonebeds.



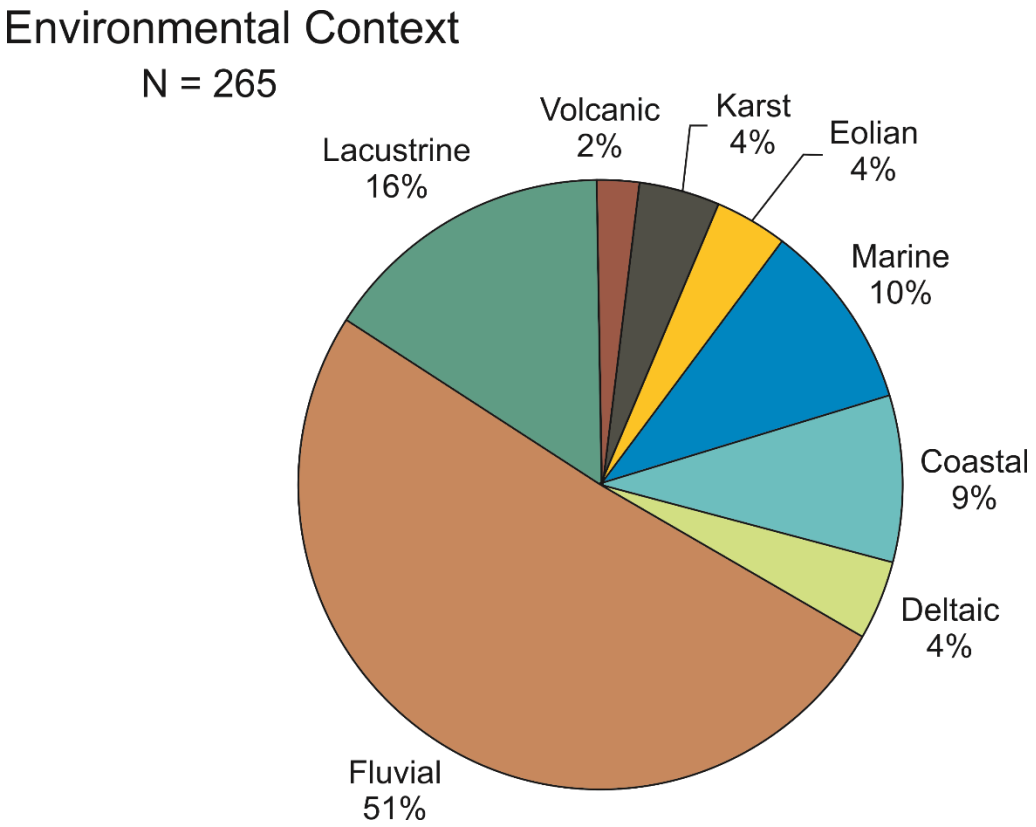
Text figure 8.9 Locality map, geology, and stratigraphic log with key vertebrate taxa found within Qujing, Yunnan Province, Southwestern China (taken from Zhang et al. 2010).

It is clear that during the late Silurian, at numerous locations across the planet; deposits rich in vertebrate material was being laid down; however, of these numerous deposits only a few are bonebeds or regarded as bonebeds by some workers. When looking at bonebeds over time the Silurian has one of the lowest abundances of bonebeds (Text-fig. 8.10). This is due to several factors.



Text Figure 8.10 The distribution of bonebed occurrences through the Phanerozoic (taken from Behrensmeyer 2007).

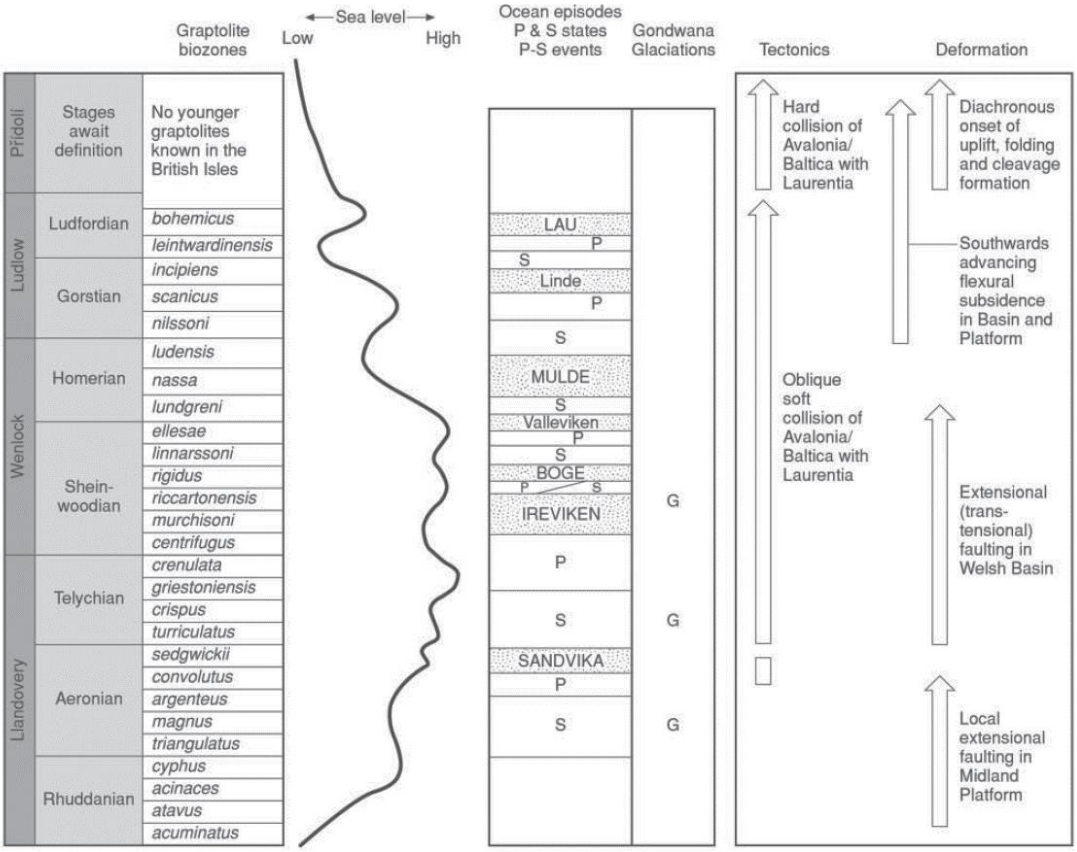
The Silurian is the shortest period of the Phanerozoic (duration c. 25 my). This means that there is far less time for bonebeds to have formed. Also, the taxa present are less likely to deposit vast quantities of the hard parts necessary for the formation of a bonebed. Consider a cartilaginous agnathan like a thelodont vs a teleost fish with a larger more robust endoskeleton. Another factor is the consideration that many of the complex ecosystems that vertebrates inhabited in the late Palaeozoic/Mesozoic/Cenozoic, were not occupied during the Silurian Period (Text-fig. 8.11). However, the most probable driving force for why Silurian bonebeds are rare and only appear at the end of the Silurian is due to sea level. For the majority of the Silurian sea level was high (Cherns et al. 2006), with only the late Silurian experiencing a rapid sea level fall. It is often in these transgressive/regressive sequences that bonebeds are likely to form (Rogers et al. 2007).



Text Figure 8.11 Pie chart of percentage of bonebeds found in particular environmental contexts. Some would have been unable to support of the formation of bonebeds during the Silurian due to lack of vertebrates that could occupy such settings, e.g. aeolian and lacustrine (taken from Behrensmeyer 2007).

8.5.2 The British Silurian Bonebeds

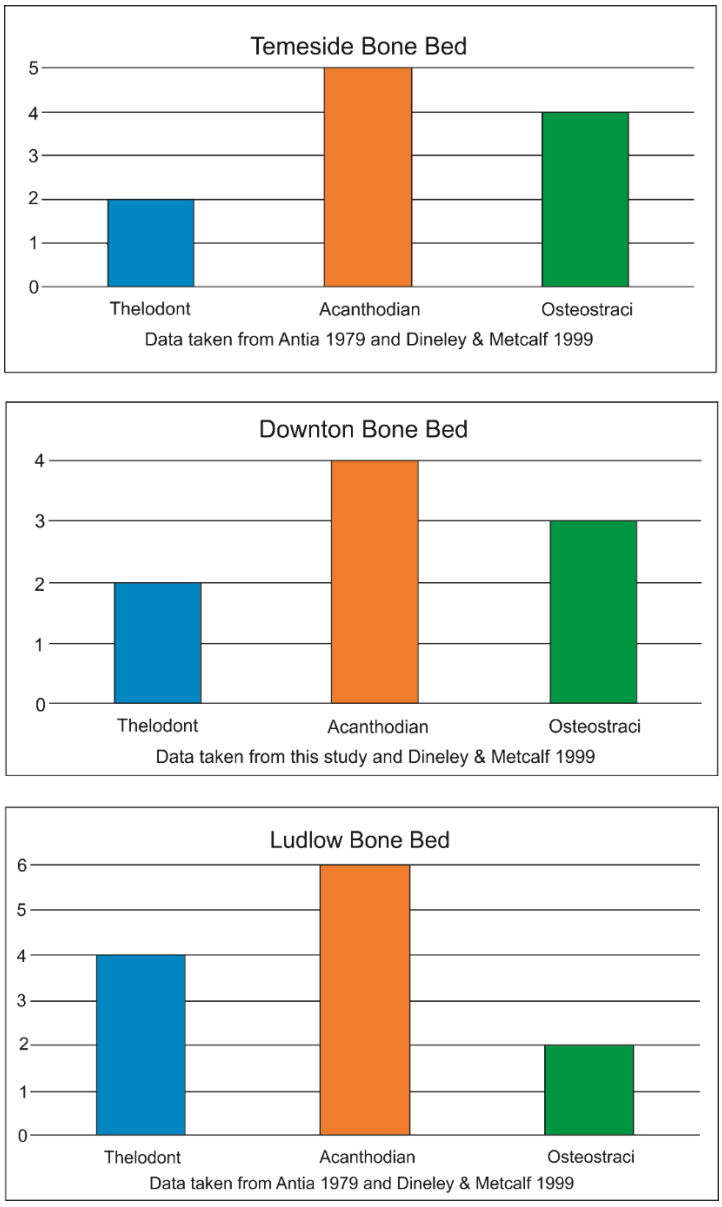
The most striking aspect of this Silurian bonebeds review is that the U.K. has a relative abundance of Silurian bonebeds. Of the five known Silurian bonebeds, three are from the U.K. This makes the Welsh Borders unique as it records three intervals of time during which bonebeds formed providing a sample of life on Earth from the late Silurian of what was Avalonia. When looking at the environmental interpretations for the three bonebeds, it is clear that a trend is seen from a transgressive to a regressive sequence that is recorded in the upper Silurian of the Welsh Borders (Text-fig. 8.12) (Cherns et al. 2006; Haq and Schutter 2008; Loydell and Frýda 2011).



Text figure 8.12 Sea-level curve for the Silurian, showing the transgression within the Ludfordian before sea level declines into the Přídolí reflecting the environments recorded by the Welsh Border bone beds. Oceanic episodes are also recorded including Primo (P) and Secundo (S) events, including the Lau event, and the tectonics and deformation (modified from Cherns et al. 2006).

The Silurian was a period of significant change for life on Earth and these three bonebeds record life in Avalonia at this time and how it adapted to changes in sea level and oceanic events. Since they are geographically close to each other as well as stratigraphically close, with the LBB and the DBB being within the DCSF and the TBB being within the overlying Temeside Formation, a comparison can be made of the vertebrate diversity within each bonebed (Text-fig. 8.13).

What can be seen is that acanthodians remain the most diverse group in all the bonebeds while the diversity of Osteostraci steadily increases over time, and the thelodonts decrease and then maintain low diversity.



Text figure 8.13 Bar charts showing the diversity of each vertebrate group found in the Welsh Borders bonebeds.

These data clearly show that the vertebrate turnover described by Eriksson et al. (2009) in the mid Ludfordian of Gotland (Chapter 4, section 4.4.1, Text-fig. 4.14) as a result of the Lau Event, is not seen in the Welsh Borders. These data also support the recent findings of Sallan et al. (2018) who found evidence that through the middle Palaeozoic "Robust fishes shifted shoreward, whereas gracile groups moved seaward". This can be seen in the bonebeds of the Welsh Borders where the bonebeds were formed close to shore and are dominated by a higher diversity of more robust groups (acanthodians and osteostracans) while the gracile groups (thelodonts) were reduced in diversity. The higher diversity of acanthodians and thelodonts in the LBB, however, may be artificial, as a result of the bonebed being condensed and time-averaged, more so than the DBB or TBB.

9. Conclusion

9.1 Introduction

This section will conclude and summarise the findings of each chapter; it will also discuss further work that could arise from this study, before finally presenting a palaeoenvironmental reconstruction of the Downton Sea and the coastline during the late Silurian.

9.2 Sedimentology

The sedimentology of the DBB at Weir Quarry shows a deposit that represents two energy regimes. The first regime appears quiet, where planar and quasi-planar lamination of sand and silt were formed. This is followed by a phase of rapid deposition, the forming of erosive bases and a fining-up sequence where all the vertebrate fossil material is deposited. This horizon is a high energy event and is followed by a return to the prior lower energy depositional regime. As discussed within the sedimentology chapter the evidence gathered suggests that the DBB at Weir Quarry formed as a result of storms and was deposited on a lower shoreface below fair-weather wave base on the coast of the Downton Sea in a water depth of between 5 to 15 m.

9.3 Vertebrates

The vertebrates in the DBB at Weir Quarry are dominated by the thelodont *Paralogania ludlowiensis*, a shallow water demersal schooling species, while far rarer is the thelodont *Thelodus parvidens* which appears to been adapted for a demersal lifestyle above hard substrates. Although *P. ludlowiensis* is by far the most common vertebrate in the DBB, overall the thelodonts are the least diverse with only the two previously mentioned taxa being present. Less common but more diverse are the acanthodians, and the Osteostraci are also higher in diversity in the DBB than the thelodonts although the Osteostraci were not recorded from Weir Quarry. They have, however, been recorded from other localities of the DBB. The vertebrates were likely

not living on the lower shoreface; instead, they were living out on the shelf and open sea with their remains accumulating on the seafloor, but substantial storms swept the material together and deposited them upon the lower shoreface. Support for this comes from the taphonomy of the vertebrates, in particular, *Paralogania ludlowiensis*, whose denticles are often chipped and abraded, which is suggestive that the denticles were exposed to high energy and transport. The overall low diversity of vertebrates is indicative of a restrictive environment.

9.4 Invertebrates

The invertebrates of the DBB are low in diversity with the Bivalvia and Gastropoda being represented by only one taxon each; others, like the ostracods and the brachiopods, are slightly more diverse. The invertebrates indicate a similar depositional setting to that suggested by the sedimentology and the vertebrates. The bivalve *Modiolopsis complanata* is disarticulated and found both individually and in a pavement, indicating that the valves were transported. The gastropod *Turbocheilus helicites* is found within the storm horizon. The ostracods are all disarticulated, single valves. The Leperdita, however, are articulated. This likely reflects that they were living on or close to the lower shoreface, and thus were not transported far enough or for a sufficient duration that the valves became disarticulated. The brachiopods are also disarticulated and found often as fragments but occasionally are found complete. These data once again support the environmental setting of the Downton Sea being a restricted environment. There are fragments of eurypterid cuticle, likely to have been broken and fragmented in the turbulent waters associated with the formation of the DBB at Weir Quarry.

9.5 Palaeobotany and Palynology

The DBB at Weir Quarry not only contains a record of the aquatic life during the mid-Ludfordian but also records the terrestrial plants that were growing on the land adjacent to the Downton Sea. There is little in the way of palynomorphs possibly due to the proximity of the shore, although this may have been a greater distance than first assumed due to storm activity. Instead, the palynological residues are dominated by dispersed organic matter (DOM), fragments of plant and fungal material. Amongst this DOM are fairly complete examples of the early plants like *Cooksonia pertoni*, *Hollandophyton colliculum*, *Synorisporites downtonensis* and the fungus *Nematothallus pseudo-vasculosa*. Many of the plants/fungi are preserved in exquisite detail, despite their age; this is due to low-temperature wildfires causing charcoalification of the organic matter. The presence of wildfires and possible desiccation of the plants before being burnt infers dry periods in the climate. The diversity of the plants, fungi and kin is higher than those organisms that were living in the Downton Sea, and this is because only the sea was a restricted environment.

9.6 Ichnology

Like the vertebrates and invertebrates, the trace fossils within the DBB show a low diversity, with only two recorded: *Teichichnus* sp. and *Planolites* sp. However, these two taxa, when found together, indicate two specific environmental conditions, fluctuating salinity and dysaerobia (low oxygen). These environmental factors would have resulted in a restricted and stressed environment which is reflected in the low diversity of the vertebrates, invertebrates and trace fossils. Within the palynology residues were found possible coprolites of terrestrial invertebrates, whose body fossils have been recorded from other deposits of coeval age as well as from below and above the DBB. The presence of these coprolites, indicates that the terrestrialization of the invertebrates was underway at this time.

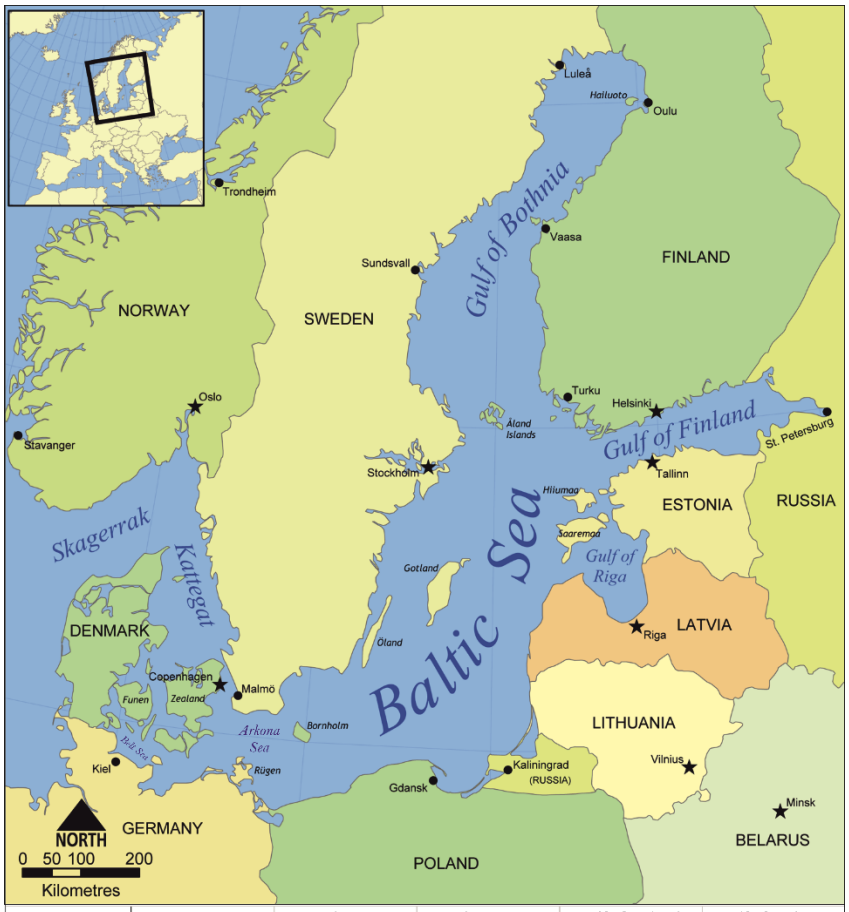
9.7 Silurian bonebeds

Bonebeds within the Silurian are currently known only from the upper Silurian and recorded only from the northern hemisphere. It has been shown recently (Sallan et al. 2019) that these shallow marine, restricted deposits were vital for the diversification of the early fishes which would later give rise to other vertebrate groups, thus underlining the importance of the DBB and other late Silurian bonebeds in our understanding of evolutionary development. These deposits are also significant as they often record the terrestrial ecosystems that were developing at this time, further emphasising the importance of these beds to our understanding of life on Earth during the late Silurian.

Throughout the study of this bonebed, discussion of what a bonebed is, and considering the various types of bonebed currently recognised, it seems clear that the blanket term of bonebed may not be appropriate for the DBB and possibly other vertebrate deposits of a similar character. There are two possible classifications in current use that could be applied the the DBB which are 'microfossil bonebeds', which show a relative concentration of fossils where the majority (≥75%) elements are ≤5 cm in maximum dimension (Eberth et al. 2007), and 'bone sands' for those comprising fossil elements of ≤4 mm (Rogers and Kidwell 2007). If classifying the DBB on the Weir Quarry site alone it might be more accurate to the reference to it as the Downton Bone Sand; however, other localities (e.g. Downton Castle Bridge) have far larger bioclasts than seen at Weir Quarry. This difference in the standard size of vertebrate material may skew the classification towards a microfossil bonebed, and perhaps more work is needed to clarify this. It would be arrogant to assume based on the work carried out here alone that the naming convention could be overturned; however, it is with a recommendation that in future studies the DBB should be referred to as the Downton Bone Sand (DBS). It should also be stated that the reclassification of the DBB to the DBS, does not suggest that is subordinate to a bonebed deposit. This is simply a reflection of the average grain size of the vertebrate fossils that the deposit contains (however, for convenience, the abbreviation DBB will continued to be used in the remainder of this thesis).

9.8 Palaeoenvironmental interpretation

The DBB was laid down in the shallow Downton Sea which formed in the Welsh Basin during the late Silurian; this was the remnants of the Iapetus Ocean which had begun to close earlier in the Silurian. Due to the Downton Sea being cut off from the main seaway it resulted in the sea becoming restricted; evidence for this restricted sea comes from the fossils which indicate a low diversity. A modern analogue for a restricted sea comes from the Baltic Sea (Text-fig. 9.1) in which the cause for the decline in diversity is due to changes in salinity.

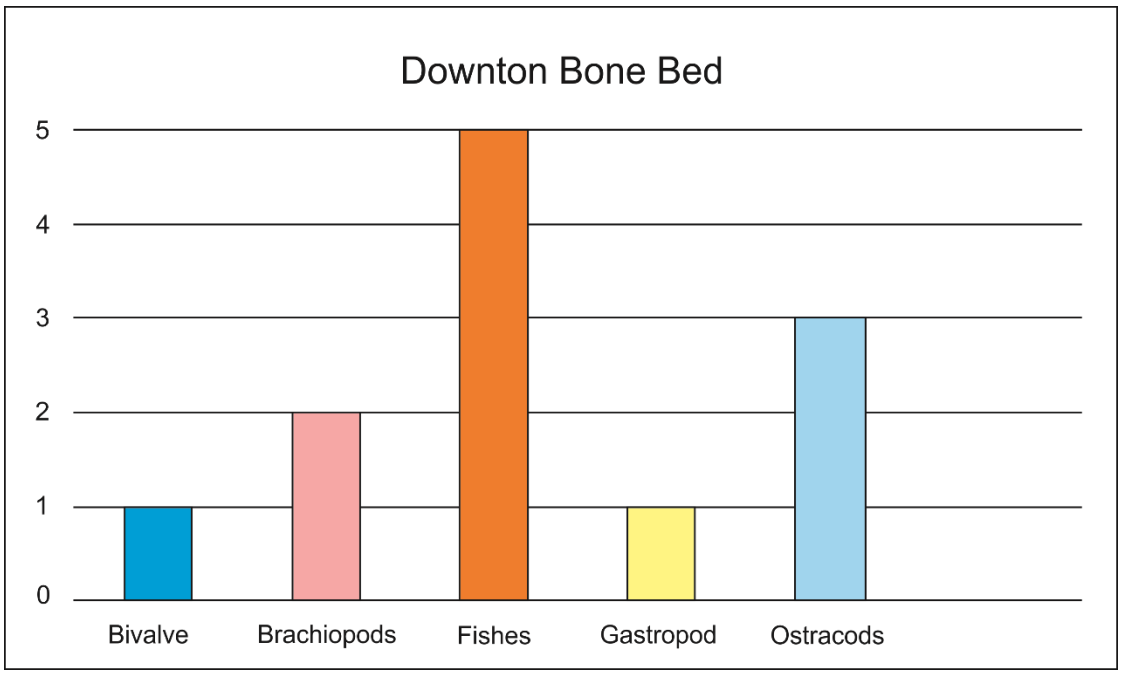


	Kattegat	Belt Sea	Arkona Sea	Gulf of Finland	Gulf of Bothnia
Salinity (%)					
Bottom	30-34	14-30	13-17	4-7	4-7
Surface	20-30	10-16	7-10	c.5	3-6
Marine groups					
Hydroids	c.47	36	21	1	x
Polychaetes	193	147	15	3	x
Bivalves	92	34	24	4	x
Amphipods	132	c.52	17	5	x
Decapods	64	c.25	5	2	x
Fishes	75	55	30	22	x

Text figure 9.1 Map of the Baltic Sea (modified form NormanEinstein wiki commons 2006) table below indicating the diversity of marine groups in different parts of the Baltic Sea (modified from Segerstråle, 1957).

What can be observed from the Baltic Sea example is as sample points move further away from the North Sea, the diversity of marine fauna decreases, and this relates to a lowering in salinity. It should be noted that in the Gulf of Finland, the diversity of fish is much higher than that seen in the DBB. This difference in diversity most likely reflects the comparison with a modern example with a fossil deposit and all of the issues surrounding the completeness of the fossil record. Also, it should be noted that modern teleosts have evolved more adaptations to living in brackish conditions compared to Silurian faunas which did not venture into fresh water until the Devonian (Downs et al. 2016). One of the key groups to observe in a palaeoecological study are the invertebrates, many of which are immobile so give a better indication of the environmental settings that they are found in. Brenchley and Harper (1998) state that "although diversity is generally low in brackish and hypersaline facies, fossils of a small number of species may be abundant and occur as crowded bedding plane assemblages". This description is identical to what is observed with the DBB and other parts other PSM, in relation to the bivalve, gastropod and ostracods. It is also noted by Brenchley and Harper (1998) that "while many brackish water species tend to be small and stunted" (this is seen in the brachiopods within the DBB), "if the species are adapted to the brackish conditions they might be more substantial". Another line of evidence comes from the trace fossils, which were discussed in Chapter 7. The presence of only *Teichichnus* and *Planolites* points to two environmental settings, brackish/restricted and dysaerobic. While there is no reason why both of these settings cannot be present, it is essential to consider both to see if either fits better with the current understanding based on other evidence. It has been suggested that one reason for the low diversity of the fauna in the DBB at Weir Quarry is due to low oxygen levels (Prof. A. Gale pers. comm. 2014). The cause of this low oxygen is assumed to be from the microbial break down of the plant matter which is found spread across many bedding planes of the DBB at Weir Quarry. The example used by Gale (pers. comm. 2014) was that leaves in a pond which are broken down by microbial decay reduce the oxygen in surrounding water through respiration of the microbes. While this would fit nicely, as clearly there is a high volume of plant material present in the DBB at Weir Quarry, and this material would be sat on the sediment surface and through microbial breakdown would, in turn, lower the oxygen levels resulting in the lower diversity observed in the other fossil groups, however this does not fit with the palaeobotanical

evidence. The preservation of the plants as discussed in Chapter 6 is as a result of charcoalification from low-temperature forest fires, which allowed them to resist both compaction and chemical breakdown. It also means that they were able to resist microbial breakdown, suggesting that dysaerobic conditions may not have been present in the DBB. This leaves only the *Teichichnus* and *Planolites* diversity indicating a brackish/restricted setting. This has been demonstrated through the other lines of evidence presented here, so when comparing the overall fauna diversity of the DBB (Text-fig. 9.2) it appears to have parallels with what is recorded from the restricted Baltic Sea (Segerstråle 1957).

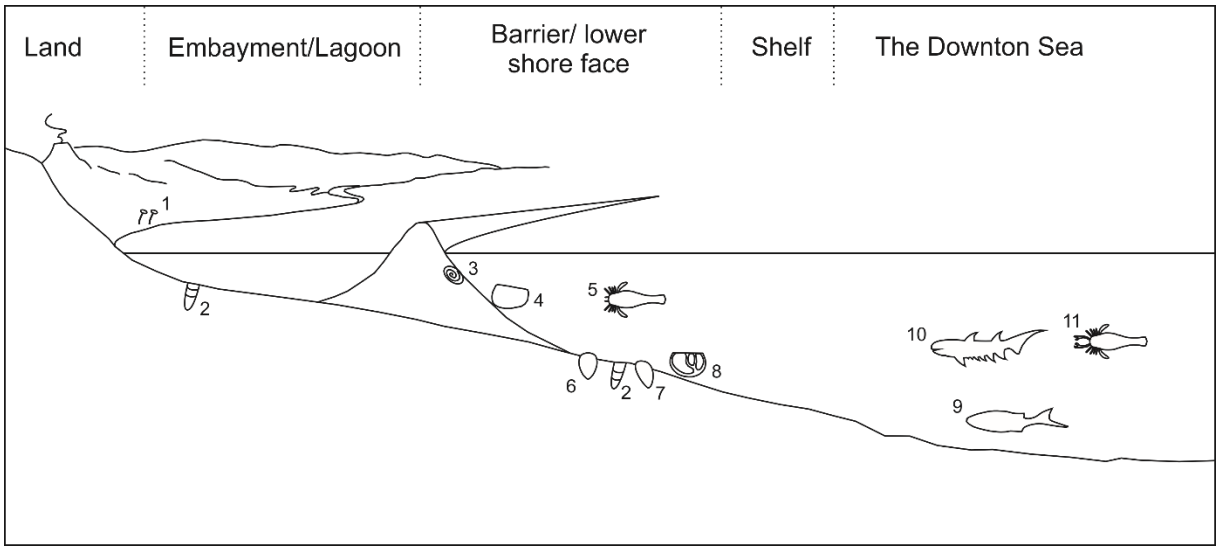


Text figure 9.2 Graph showing the total diversity of groups seen in the DBB.

The type of deposit that the DBB represents is essential in reconstructing the palaeoenvironment. Frequently this thesis has mentioned that the fauna and flora of the DBB are mostly allochthonous having been transported and buried together. By examining all of the groups individually a model can be produced (Text-fig. 9.3) that can infer the life positions of the taxa found in the DBB.

What is shown is that the thelodonts and acanthodians on the shelf and it likely that the pterygotid eurypterids would also frequent this part of the Downton Sea (Manning and Dunlop 1995), while many of the invertebrates were most likely living closer to shore before being deposited together.

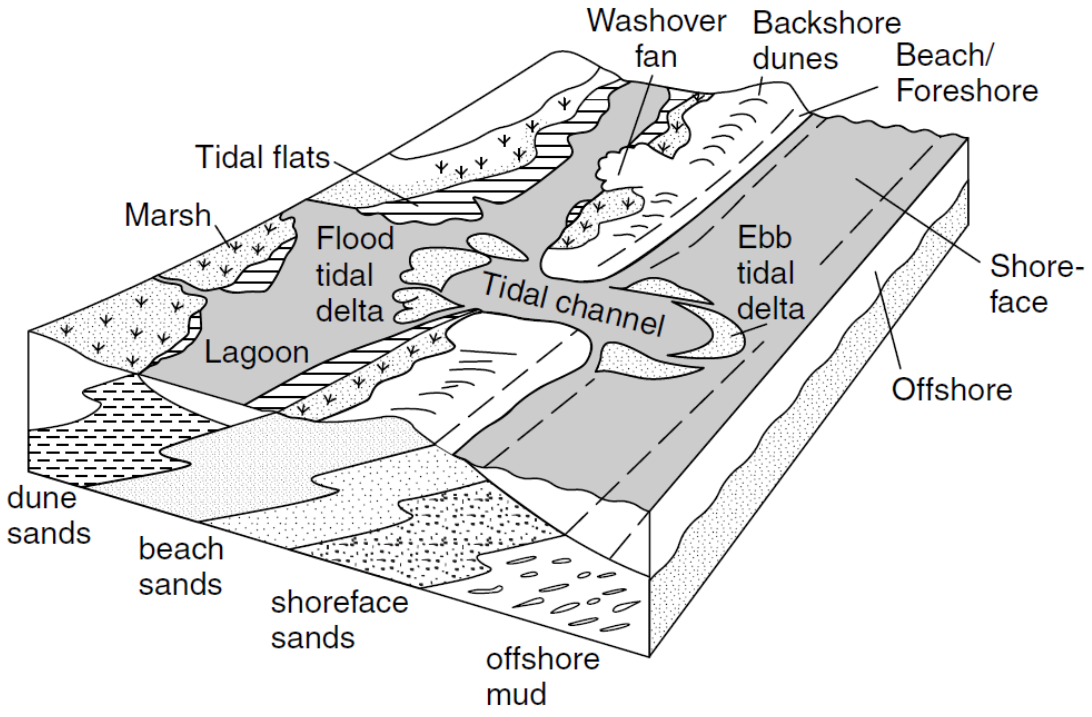
Because of the preservation and taphonomy of the fossils recorded within the DBB, it is suggested that over time material accumulated on the seafloor. This material was then picked up by large storms and dumped along the coastline and, at Weir Quarry, on the lower shoreface.



Text figure 9.3 Ecological composition of fauna and flora in the DBB, showing life position of taxa (modified from Siveter 1984): 1, organic-walled macrofossils. 2, trace fossils. 3, *Turbocheilus helicites*. 4, leperditiids. 5, eurypterid (Hughmilleriidae). 6, lingulate brachiopods. 7, *Modiolopsis complanata*. 8, *Londinia arisaigensis*. 9, thelodont. 10, acanthodian. 11, eurypterid (Pterygotidae).

Evidence for these storms comes from the sedimentology and the established literature; this evidence for storms, combined with climatic interpretations made previously (Allen 1974) allows for a climate cycle to be inferred. It suggests that the Downton Sea during the late Silurian was affected by a seasonal climate: a dry season, which would cause the desiccation of the flora on land, as well as a possible reduction in freshwater input into the Downton Sea increasing the salinity. This would have been followed by a wet season, the early onset of which may have caused lightning strikes which could have triggered the wildfires recorded in the fossil record, before rains flushed the charcoalified material out to sea. This increased freshwater input would have then potentially decreased the salinity, and it is this fluctuation in salinity that may have led to the reduced faunal diversity, as it would have been difficult for many organisms to adapt to these frequent fluctuations. Large storms would scour the seabed picking up various bioclasts before being deposited on the coastline.

An aspect of this project and mentioned in the further work section of this chapter is the difference in the character of the DBB across the Welsh Borders and beyond. Certainly, it lacks the consistency seen in the LBB. It is also reflected in the interpretations of the environment based on different fossil communities associated with the strata, ranging from a marine to brackish setting (Turner 1999), restricted lagoonal setting (Bradfield 1999) and a lower shoreface, found in this study. One reason for this variation in interpretations is the acceptance that when the DBB was laid down, it was upon a dynamic coastline, with various environments within a localised geographic area. This concept is demonstrated in Tucker (2003) (Text-fig. 9.4), which shows a marine shoreline environment and the variety of environments found close to one another, such as a lower shoreface and a lagoon.

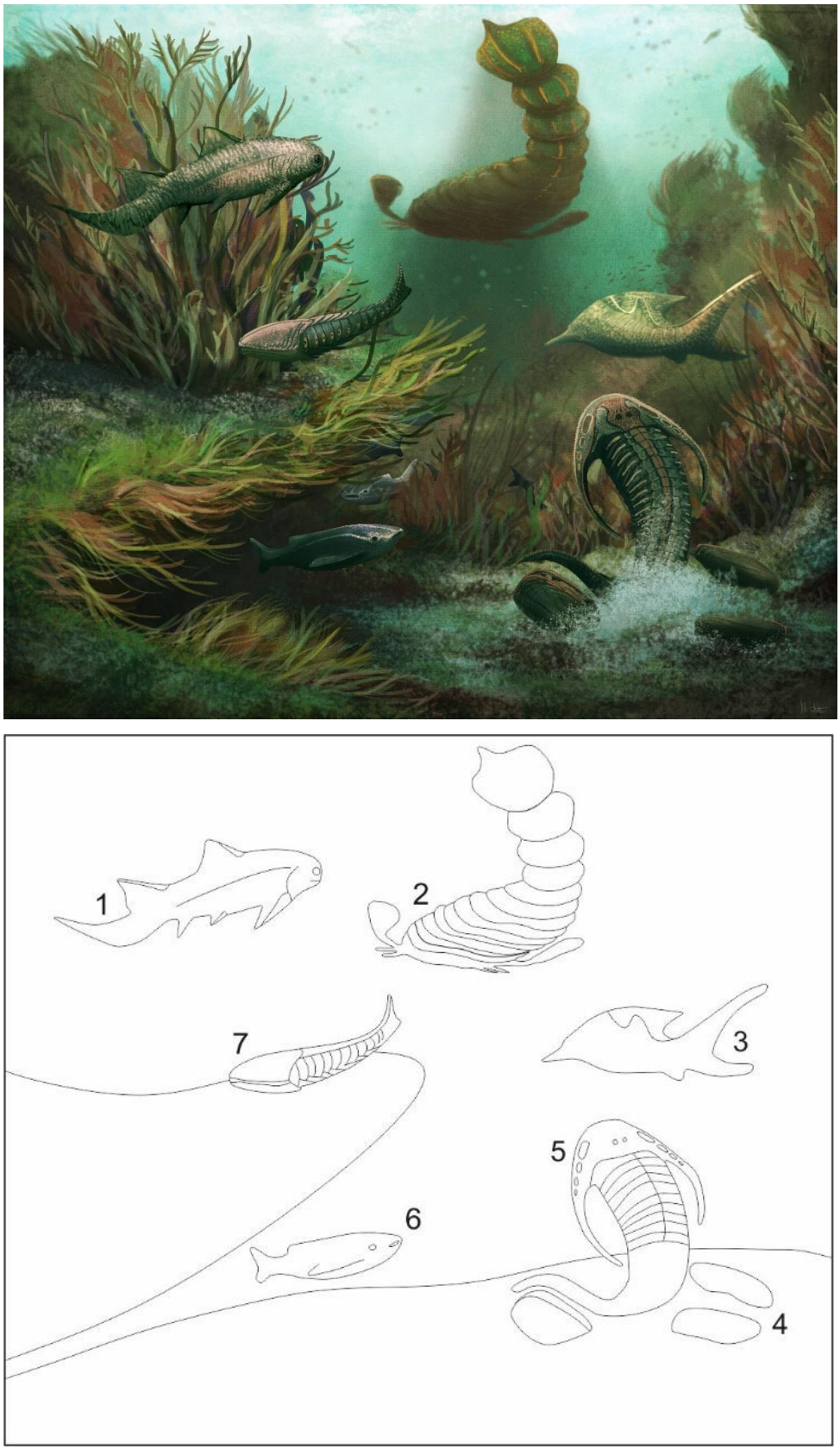


Text Figure 9.4 Facies model for a marine shoreline environment (taken from Tucker 2003).

This proximity of different environmental settings could account for the variation in the character of the DBB across its range as it was not deposited in the same setting everywhere; for example, Weir Quarry represents a lower shoreface, while the material from Downton Castle Bridge might represent a beach or foreshore, while Linley Brook was perhaps a lagoon.

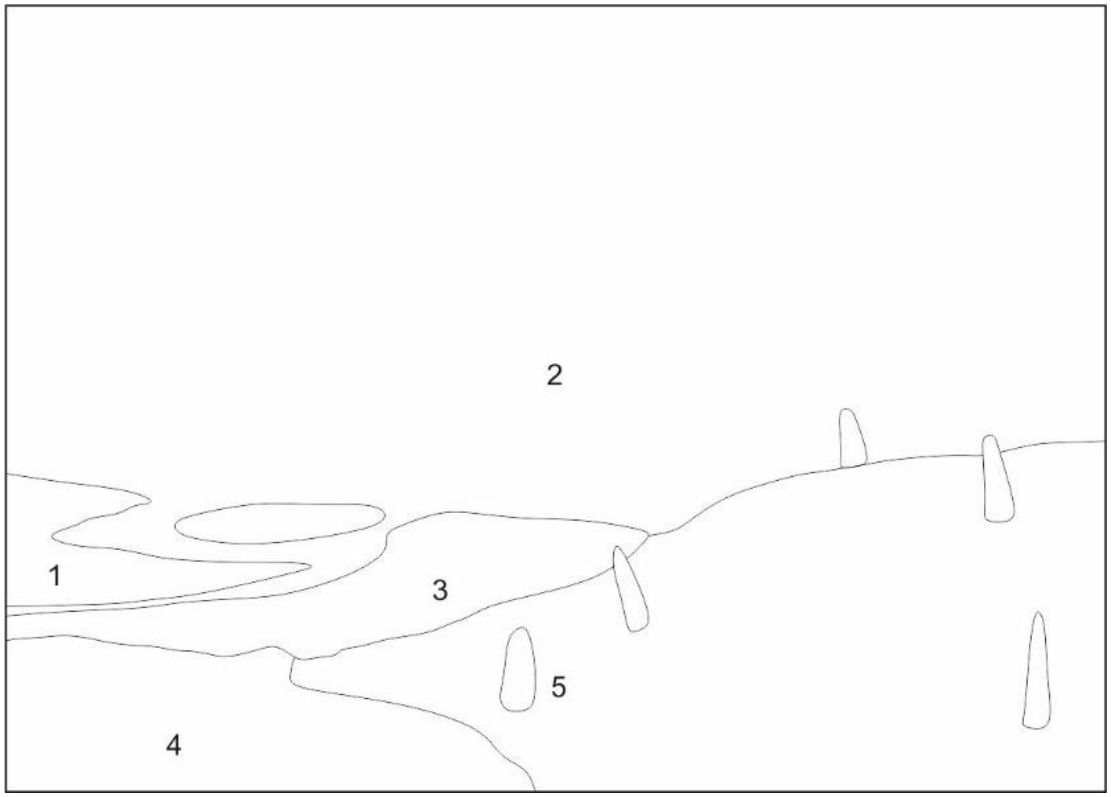
In conclusion, the fossil content of the DBB at Weir Quarry has been recorded; it consists of a low diversity assemblage of various groups of organisms. The vertebrates found are the thelodonts *Paralogania ludlowiensis* and *Thelodus parvidens*. While the acanthodians are rare within the DBB at Weir quarry they appear to have been more diverse and include the taxa *Gomphonchus* sp., *Nostolepis* sp., Acanthodii sp. and the enigmatic *Onchus murchisoni*. The invertebrates also show a similar low diversity with only one bivalve (*Modiolopsis complanata*) and one gastropod (*Turbocheilus helicites*) present respectively in the DBB at Weir Quarry. The brachiopods show diversity of two taxa: *Tunisiglossa cornea* and *Lingula missendenensis*. The ostracods are slightly more diverse with *Frostiella groenvilliana, Londinia arisaigensis* and a non-palaeocope being recorded. Also recorded is the bivalved arthropod *Leperditia* sp. There is also evidence for the presence of eurypterids although the material could not be assigned at the generic level. The ichnofaunal diversity of the DBB at Weir Quarry is also low with only two taxa recorded: *Teichichnus* sp. and *Planolites* sp. This fossil evidence suggests that the environment in which the DBB formed was a restricted environment, most likely due to seasonal fluctuations in salinity.

The plants and fungi recorded from the DBB at Weir Quarry are the most diverse fossil groups found in this study. This reflects the fact that the plants and fungi were all terrestrial and thus not affected by the restricted conditions experienced by the aquatic life recorded in the DBB. The plants, fungi and allies recorded in the DBB at Weir Quarry include *Cooksonia pertoni*, *Hollandophyton colliculum*, *Synorisporites downtonensis*, *Nematothallus pseudo-vasculosa*, *Prototaxites* sp., *Pachytheca sphaerica*, phyoclasts, fungal hyphae and unidentified organic material. Within the organic residues were found possible coprolites of early terrestrial invertebrates, most likely those of a detritivore such as early millipedes.



Text figure 9.5 The Downton Sea during the mid Ludfordian, this environment represents the environment adjacent to the lower shoreface where the DBB was deposited 1) acanthodian, 2) eurypterid, 3) *Thelodus parvidens*, 4) *Modiolopsis complanata*, 5) *Sclerodus* pustuliferus, 6) *Paralogania ludlowiensis* and 7) *Archegonaspis* sp. (artwork by Dr Mark Witton).

The sedimentology of the DBB at Weir Quarry was also recorded and described; it suggests that the DBB at Weir Quarry was laid down on a lower shoreface of the shallow Downton Sea (Text-fig. 9.5). This evidence combined with the palaeontological data support a palaeoenvironmental reconstruction of a shallow sea adjacent to a marginal environment possibly with barriers and sand bar before reaching the coast. In the Downton Sea a high diversity of organisms was present; however, within each respective group, diversity was low. This low diversity reflects a dynamic climate, that may have been seasonal with dry seasons where plants that were living on the surrounding coastline (Text-fig. 9.6) and were likely to have been desiccated. This dry season would have likely meant a reduction in freshwater input into the Downton Sea, which was possibly cut off from the primary seaway, meaning that there would have been an increase in salinity during this part of the year. This would have followed by a wet season, introducing large storms to the coast of Avalonia. These storms may have caused low-temperature wildfires to spread across the land before significant amounts of rainfall would have flushed the charcoalified organic material out into the Downton Sea. This wet season would have likely caused rivers that flowed into the Downton Sea to have reduced salinity, or in places storm waves may have breached barriers increasing the salinity of parts of the coast for a short time. It was these storms that formed the DBB at Weir Quarry picking up large amounts of sediment on the seafloor enriched in vertebrate and invertebrate material before being deposited on the lower shoreface. Later, organic material settled out of suspension and was deposited within the bonebed; this was then followed by a return to the quiet sedimentation seen in the rest of the bed and the PSM.



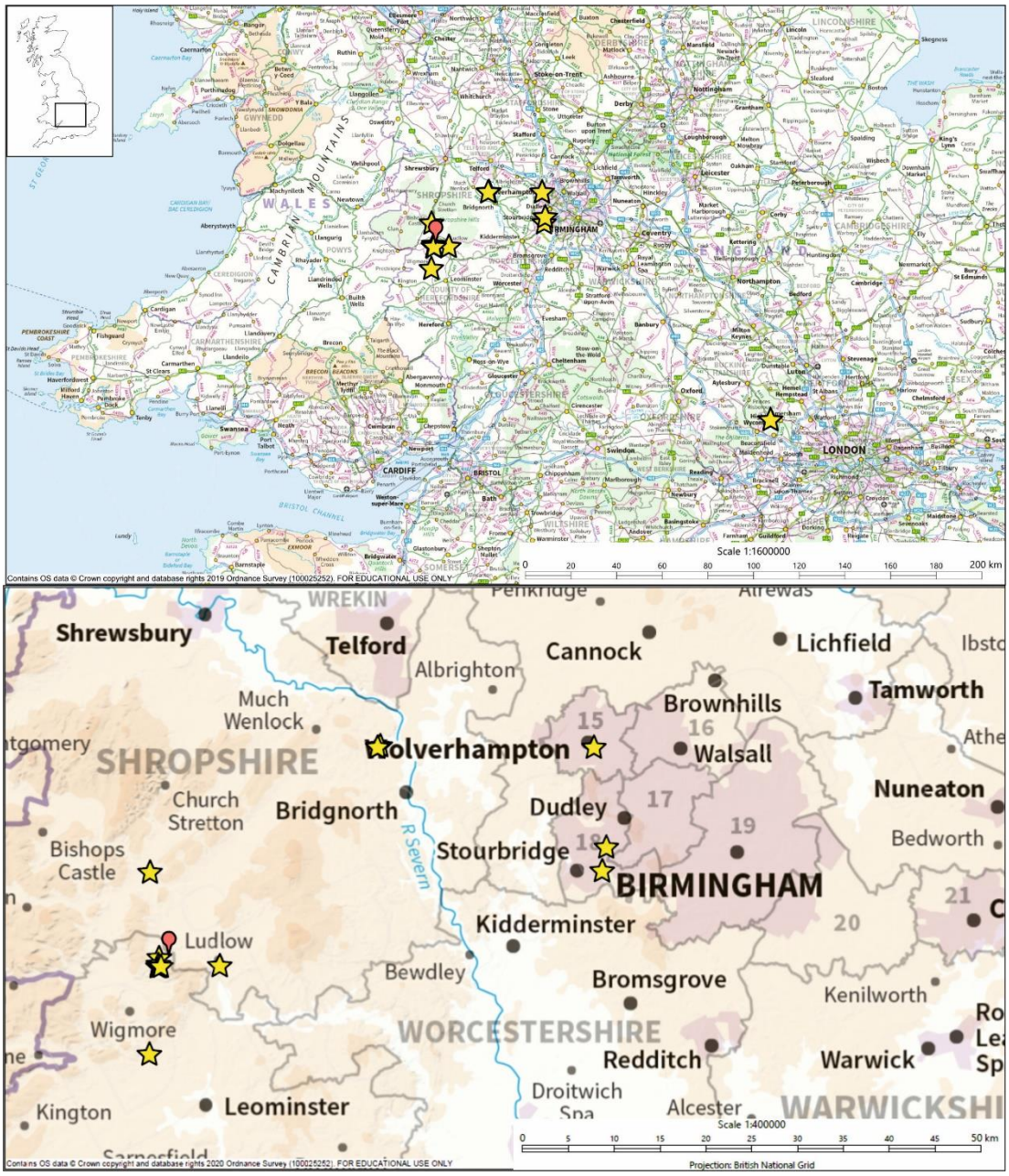
Text figure 9.6 Coast of Downton Sea during the mid Ludfordian, 1) Localized low temperature wild fires, 2) Downton Sea, 3) Rivers flowing into the Downton Sea, 4) Variety of early plants such as *Cooksonia* and 5) The fungus *Nematothallus* (artwork by Dr Mark Witton).

In summary, the DBB at Weir Quarry represents a window in a crucial time in Earth's history and an environment that was critical for the evolutionary development of early vertebrates before the "age of fish" during the Devonian. Weir Quarry also represents the only accessible locality currently known of the DBB. Other sites are either known only from ex-situ material or are no longer accessible. This study now fills a gap in our knowledge of late Silurian Welsh Borderland bonebeds and suggests that further study of these internationally rare and valuable deposits is required.

9.8 Further Work

This study had from the outset a broad scope: to record all of the fossils present in the DBB at Weir Quarry and their sedimentary context. One of the hopes was to reconstruct the palaeoenvironment of the Weir Quarry locality. These goals have been achieved; however, through the study of the DBB it was clear that there are a great many more localities that have outcrops of the DBB (Text-fig. 9.7), despite what had been previously reported (Antia 1979b). While many were investigated (most of which could not be accessed), others have not been investigated due to the constraints of the project but are recorded in Chapter 1, Table 1.1. This is a clear avenue for further study to see how these other deposits fit into the emerging image of the DBB, as many of the existing samples for these localities come only from ex-situ material. Like many projects of this nature, the more samples processed and examined the more can be found so continued sampling and processing of this bone sand would also be suggested for further work, as this may give a broader image of the taxonomic diversity, and formation of the DBB across the Welsh Borderlands and possibly beyond.

Another project after the publication of the chapters from this thesis would be to make a more in-depth comparison of the three Welsh Borderland bonebeds as they offer the unique opportunity to monitor how life adapted to the Lau Event, which comprised smaller extinction events as well as a transition to a steadily more terrestrial environment. Furthermore, in-depth studies on the LBB and TBB were last carried out more 30 years ago, so they are likely overdue for review.



Text figure 9.7 Map showing extent of the nineteen DBB localities in the U.K., the red marker indicates Weir Quarry (modified from Digimap 2019).

Appendix A. An integrated microwave technique for releasing microfossils from an indurated bone bed.

JM-TMS
Journal of Micropalaeontology

Research article

Published online October 28, 2015 doi:10.1144/jmpaleo2015-005 | Vol. 35 | 2016 | pp. 62–65

An integrated microwave technique for releasing microfossils from an indurated bone bed

Luke M. Hauser

School of Earth and Environmental Siences, University of Portsmouth, Burnaby Road, Portsmouth PO1 3QL, UK
luke.hauser@port.ac.uk

Abstract: Bone beds have often been a focus for micropalaeontological study as the high concentration of fossil material allows vertebrate palaeontologists the returns normally experienced only by nannofossil workers and palynologists. It is not always straightforward to release the fossil material within bone beds and the extraction of microfossils from the upper Silurian Downton Bone Bed is particularly challenging. Outlined here is an integrated method for processing this bone bed using liquid paraffin and a microwave oven, and a comparison in terms of quality and quantity with material recovered using other techniques. This integrated method allows for the recovery of microvertebrates, such as thelodonts, and also internal moulds of ostracods, brachiopods and early plant material.

Keywords: Silurian; Downton Bone Bed; microfossils; extraction; Welsh Borderlands

Received 12 February 2015; **accepted** 26 May 2015

The standard method to recover phosphatic microfossils, in particular microvertebrates, is to use acetic acid (CH_3COOH) (Jeppsson *et al.* 1999). This is certainly the case when recovering material from the two best known UK bone beds, the Westbury and Ludlow bone beds (Antia & Whitaker 1978; Swift & Martill 1999). However, some bone beds lack calcium carbonate cement and thus do not break down at all in acetic acid. One such bone bed is the Downton Bone Bed of the upper Silurian of the Welsh Borders. Described here is an integrated method for use on such indurated bone beds with no calcium carbonate content.

Located 1.5 m above the Ludlow Bone Bed at Weir Quarry, Downton, Shropshire, UK [SO 4560 7525], the Downton Bone Bed lies within the Platyschisma Shale Member of the Downton Castle Sandstone Formation. The Platyschisma Shale Member was long considered to be of Přídolí age, but Loydell & Frýda (2011) presented numerous lines of biostratigraphical and chemostratigraphical evidence demonstrating that it is mid-Ludfordian (late Ludlow Epoch). Another key piece of evidence indicating a Ludlow age for the Downton Bone Bed is the presence of abundant denticles of the thelodont *Paralogania ludlowiensis* (Gross, 1967). All records of this taxon from Gotland and the Baltic States are from the Ludlow Series (Miller & Märss 1999): none are from the Přídolí. Independent dating is provided by chitinozoans, e.g. in the Ohesaare core of Saaremaa, Estonia the lower Kuressaare Formation contains *Paralogania ludlowiensis* within the Ludfordian Eisenackitina lagenomorpha Biozone (Nestor 2009).

Despite micropalaeontological and palynological studies of the Platyschisma Shale Member within the last 25 years (e.g. Richardson & Rasul 1990; Miller 1995; Miller & Märss 1999), and brief mention of fossils from the Downton Bone Bed (e.g. Märss & Miller 2004), the sedimentology and fossil content of the Downton Bone Bed have not been studied in any detail (Eberth *et al.* 2007).

Sedimentology

Despite being part of the Platyschisma Shale Member (Bassett *et al.* 1982), the Downton Bone Bed is in fact an extremely well-indurated quartz arenite. Thin sections (Fig. 1) show the non-fossil component of the bed is almost completely quartz within a clay matrix. The grains are tightly packed, which is the reason why the Downton Bone Bed is such a challenge to break down. The denticle-rich bands are found in discrete horizons usually in close proximity to layers rich in plant material. They appear to have been deposited as a result of storm activity. On bedding surfaces the denticles within the bone bed can be seen to be abraded, often with parts of the crown or base missing (Fig. 2). This is important to bear in mind when assessing the damage to specimens resulting from the different extraction methods.

Methods

Other techniques assessed

In trying to disaggregate the Downton Bone Bed a number of alternative techniques were tried before the method described herein was used. The first was the mechanical method described by Rixton (1976) and Green (2001, pp. 110–112). Although this did eventually yield material, the time it took (1 month) to break down the bed made it unsuitable to use. This problem was compounded by the poor quality of the fossils recovered; the denticle shown in Figure 3a is the best example from the residue recovered and it is clearly damaged, particularly on the base which has a sharp break. The presence of the clay matrix suggested that hydrogen peroxide (H_2O_2) could be used. Although there was effervescence on the surface, the tight grain packing prevented the H_2O_2 from penetrating the rock. Freeze–thaw was also attempted using liquid nitrogen, boiling water and a microwave. This only caused the rock to split along bedding planes.

The Selfrag method is in its infancy in vertebrate palaeontology and has been used in metamorphic geology to extract accessory minerals (Giese *et al.* 2007). The method involves placing a sample, cut or split into small pieces, into a device upon which two electrical probes deliver high voltage pulses to the sample. This fragments the rock leaving the targeted grains intact. A 1 kg sample was processed using a probe gap of 20 mm, a 5 Hz pulse frequency and a 90 kV voltage. The sediment returned was sieved

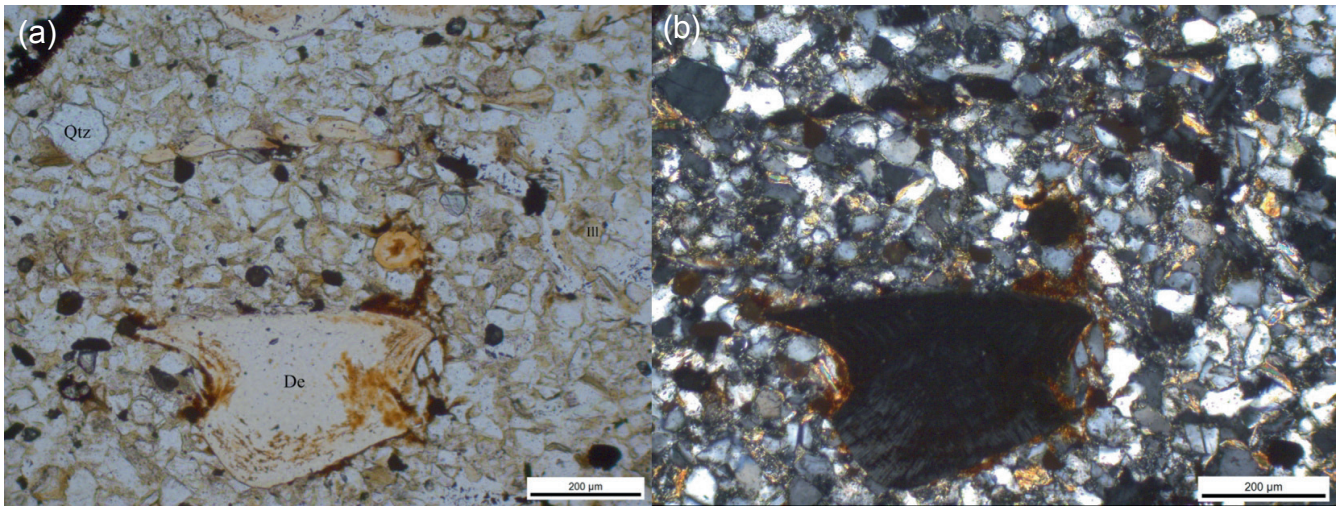


Fig. 1. Petrology of the Downton Bone Bed from a bone-rich horizon: (**a**) plane polarized light, quartz (Qtz), illite (Ill) and thelodont denticle (De); (**b**) cross-polarized light.

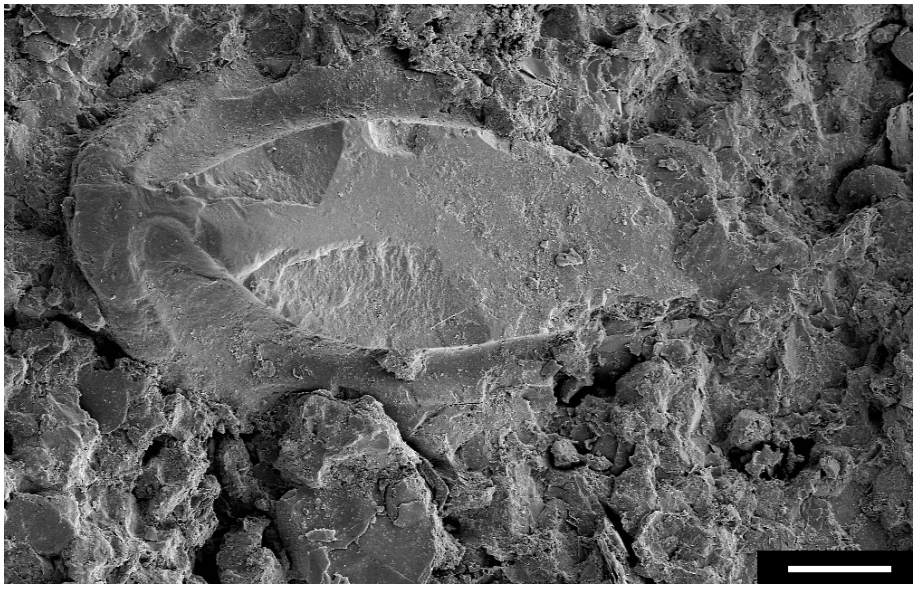


Fig. 2. *Paralogania ludlowiensis* (Gross, 1967) trunk scale in crown view, *in situ* on bedding surface. Scale bar 100 µm.

into four size fractions (500, 212, 106 and 75 µm) and then placed in sodium polytungstate (specific gravity 2.8) for heavy liquid separation using the method described by Savage (1988). The material recovered was of the same quality as that from the mechanical method (Fig. 3b). However, the quantity of fossil material recovered and the time the process took (5 min) shows that it is a far better technique than the mechanical method. A significant limiting factor for its use is cost (Table 1) so Selfrag is a non-viable option for processing numerous samples.

Pre-treatment

The same pre-treatment was conducted on all samples. The samples were washed with water mixed with 10 ml Decon 90 to remove all modern organic material. A toothbrush was used to remove any material that did not initially wash off. After washing and cleaning, the samples were left to air dry.

Health and safety

It is very important when carrying out any scientific laboratory work to consider the health and safety aspects of any procedure. For the method used, the standard laboratory practice of wearing a lab coat, latex gloves and safety goggles is recommended. When using the microwave, further precautions should be taken. The microwave must be placed in a fume cupboard to allow any fumes from the paraffin to be drawn away and, while processing the sample, the hood should be drawn down to protect the user. It is also advisable after processing each sample to allow the Pyrex plate in the microwave to cool down to ensure that the equipment operates at a safe temperature.

The paraffin expansion method

To break down the Downton Bone Bed successfully the following method was used.

1. Cut the sample into blocks with a mass of <100 g. A rock splitter can be used to take advantage of the rock's natural weaknesses. This has two benefits: (1) it will fit into the ideal container (a 200 ml Polytetrafluoroethylene (PTFE) beaker) and (2) the paraffin penetrates into smaller pieces more effectively because of their larger surface area to volume ratio.
2. Place the blocks in a large plastic bowl filled with liquid paraffin and allow to soak for 24 h.
3. Remove the blocks from the paraffin and place on paper towels to remove excess liquid; the rock should appear damp rather than dripping wet.

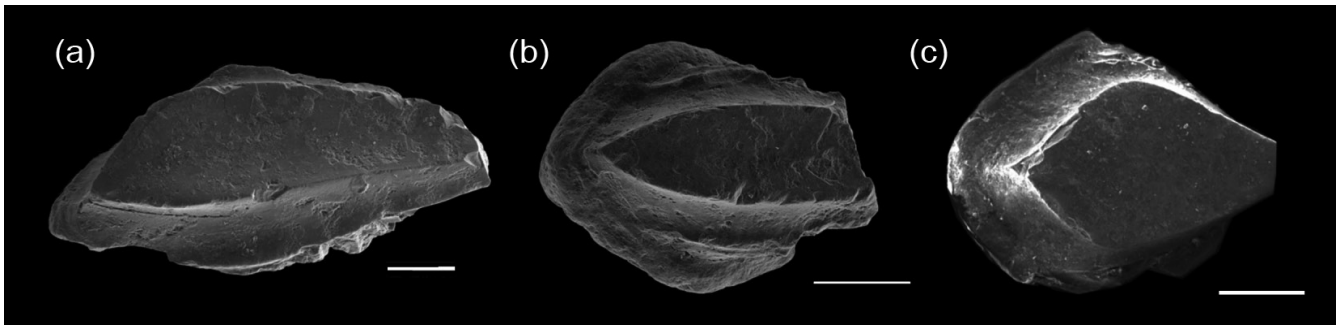


Fig. 3. Examples of the least damaged *Paralogania ludlowiensis* (Gross, 1967) trunk scales shown in crown view taken from each sample processed by the three different methods: (**a**) mechanical; (**b**) Selfrag; (**c**) paraffin expansion. Scale bar 200 µm.

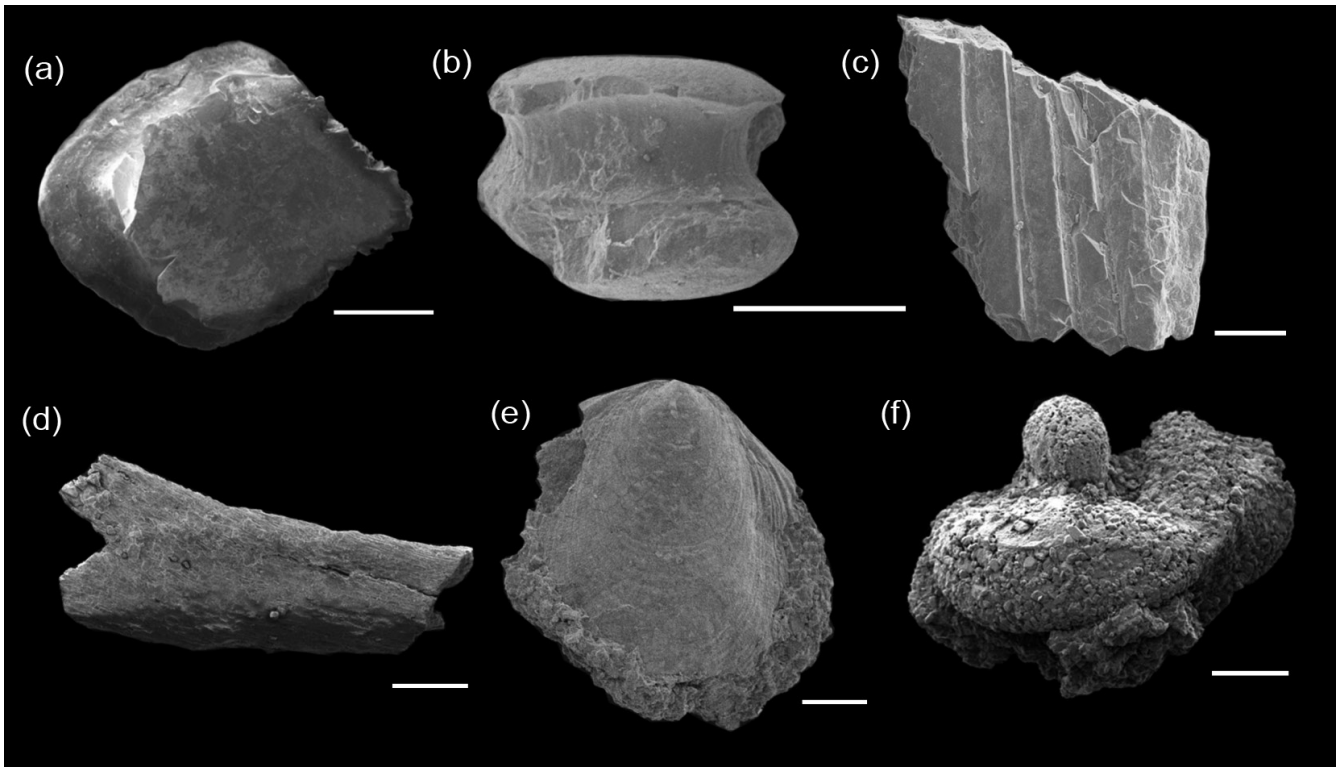


Fig. 4. Material produced using the paraffin expansion method showing preservation and the wide range of material released: (**a**) *Paralogania ludlowiensis* (Gross, 1967) trunk scale in crown view; (**b**) *Thelodus parvidens* (Agassiz, 1839) trunk scale in lateral view; (**c**) indeterminate acanthodian fragment in lateral view; (**d**) *Hollandophyton colliculum* (Rogerson *et al.*, 2002); (**e**) lingulid brachiopod valve exterior; (**f**) internal mould of the ostracod *Frostiella groenvalliana* (Martinsson, 1963). Scale bars represent 300 µm.

Table 1. *Comparison of the three methods used in this study*

	Techniques		
	Mechanical	Selfrag	Paraffin expansion
Time to process 1 kg of sample	1 month	5 minutes	3 days
Total amount of rock broken down (%)	40	100	60
Quality of fossil material extracted	Poor	Moderate	Good
Cost to process per samples (£)	13	384	14
Types of fossils recovered	Fish, brachiopods	Fish, brachiopods	Fish, brachiopods, ostracods, plants

4. Place a block inside a 200 ml PTFE beaker (chosen because they can withstand a high temperature).
5. Once the block has been placed inside the beaker, place a Pyrex watch glass on top to act as a lid to prevent fragments of rock from escaping from the beaker.
6. Place the beaker with watch glass into the microwave and turn on for 2 min at full power (800W).
7. Carefully remove the beaker and pour its contents into a large bowl of cold water to quench the sediment and any remaining rock fragments.
8. After the processing is complete, pour the sediment through sieves of various sizes. For the purpose of this study, sieve sizes of 2.36 mm, 1.70 mm, 500 µm, 212 µm, 106 µm and 75 µm were used.

9. Wash processed sample fractions in distilled water until clean and then place in an evaporating dish to air dry.
10. Once the sediment is dry, further separate the material using heavy liquids. Sodium polytungstate (SPT) with a specific gravity of 2.8 is commonly used to separate the phosphatic elements from the detrital grains (Savage 1988). However, it is also possible to pick the fossils directly from the residue.

A major advantage of this cheap and simple method is that a wide diversity of material can be recovered including not only vertebrates, but also invertebrates and plants (Figs 3c and 4).

Discussion

The method described herein represents a new combination of aspects of a number of previously used methods (Jones 1994; Green 2001). This paraffin expansion method for processing indurated bone beds described herein is similar to the petroleum spirit method described in Green (2001, p. 324). However, there are some key differences. The first is that the petroleum spirit method is recommended for less indurated rocks, such as shales (Green 2001). The petroleum spirit method also uses boiling water to break the rock down further, whereas the paraffin expansion method uses a microwave to achieve a much quicker result. The Downton Bone Bed has one major difference to other bone beds, which is the presence of organic-rich layers. This appears to be the key to the method's success. Paraffin is a solvent which subtly breaks down some of the organic matter within the bed creating more pore space. However, the process is not totally destructive to plant material as some has been recovered and does not appear damaged (Fig. 4d). The rapid heating of the paraffin to its boiling point of 280–350°C allows the build-up of volatiles and other gases within the pore spaces. This results in the sample being mechanically disintegrated by the gases in a process of vaporization, which is different from the petroleum spirit method which breaks the bonds within the clays, liberating the fossils from the rock. However, improvements can be made as not all of the sample was broken down (Table 1). To investigate why, these remaining indurated pieces of the samples were reprocessed. After a second cycle, the sample remained indurated. This was because the first round of processing had removed all the organic material; without this the paraffin has nothing to break down and in turn has no extra pore spaces to allow the gases to mechanically break the rock down. However, it is possible that the remaining aggregates could be subjected to other mechanical techniques having been weakened by the initial processing. Despite this, it is clear that the paraffin expansion method is the least destructive method to the fossils (Fig. 4; Table 1), which shows the range of taxa recovered. This includes complete brachiopods, which are usually broken when recovered using other methods. However brachiopods that were fragmented pre-deposition are also found in the paraffin expansion residue.

Acknowledgements and Funding

The author thanks C. Lyons of Downton Estates Ltd for permission to visit Weir Quarry, D. Loydell for editing and advice, A. Weh and Selfrag for running a test sample, E. Dyer and R. Hing for technical assistance and E. Hart for editing, support and discussion. Also thanked are the two referees, O. Green and C. G. Miller, for their helpful and constructive comments and advice. This paper is a contribution to the International Geoscience Programme (IGCP) Project 591 – The Early to Middle Palaeozoic Revolution.

Scientific editing by Giles Miller

References

Agassiz, L. 1839. Fishes of the Upper Ludlow rock. *In*: Murchison, R.I. (ed.) *The Silurian System, Founded on Geological Researches*. Richard & John E. Taylor, London.

Antia, D.D.J. & Whitaker, J.H.McD. 1978. A scanning electron microscope study of the genesis of the upper Silurian Ludlow Bone Bed. *In*: Whalley, W.B. (ed.) *Scanning Electron Microscopy in the Study of Sediments*. Geo Abstracts, Norwich, 119–136.

Bassett, M.G., Lawson, J.D. & White, D.E. 1982. The Downton series as the fourth series of the Silurian system. *Lethaia*, **15**, 1–24.

Eberth, D.A., Shannon, M. & Noland, B.G. 2007. A bonebeds database: Classification, biases, and patterns of occurrence. *In*: Rogers, R.R., Eberth, D.A. & Fiorillo, A.R. (eds) *Bonebeds: Genesis, Analysis, and Paleobiological Significance*. University of Chicago Press, Chicago, IL, USA, 132–219.

Giese, J., Seward, D., Gnos, E. & Kurz, D. 2007. Comparative apatite fission track study of conventionally versus Selfrag Lab fragmented samples. *Geochimica et Cosmochimica Acta*, **71**, A322.

Green, O.R. (ed.) 2001. *A Manual of Practical Laboratory and Field Techniques in Palaeobiology*. Springer, The Netherlands.

Gross, W. 1967. Über Thelodontier-Schuppen. *Palaeontographica*, **A127**, 1–67.

Jeppsson, L., Anehus, R. & Fredholm, D. 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. *Journal of Paleontology*, **73**, 964–972.

Jones, R.A. 1994. The application of microwave technology to the oxidation of kerogen for use in palynology. *Review of Palaeobotany and Palynology*, **80**, 333–338.

Loydell, D.K. & Frýda, J. 2011. At what stratigraphical level is the mid Ludfordian (Ludlow, Silurian) positive carbon isotope excursion in the type Ludlow area, Shropshire, England? *Bulletin of Geosciences*, **86**, 197–208.

Märss, T. & Miller, C.G. 2004. Thelodonts and distribution of associated conodonts from the Llandovery–lowermost Lochkovian of the Welsh Borderland. *Palaeontology*, **47**, 1211–1265.

Martinsson, A. 1963. The concealed Silurian of the Baltic area. *Geologiska Föreningen i Stockholm Förhandlingar*, **84**, 539–545.

Miller, C.G. 1995. Ostracode and conodont distribution across the Ludlow/Přídolí boundary of Wales and the Welsh Borderland. *Palaeontology*, **38**, 341–384.

Miller, C.G. & Märss, T. 1999. A conodont, thelodont and acanthodian fauna from the lower Přídolí (Silurian) of the Much Wenlock Area, Shropshire. *Palaeontology*, **42**, 691–714.

Nestor, V. 2009. Biostratigraphy of the Ludlow chitinozoans from East Baltic drill cores. *Estonian Journal of Earth Sciences*, **58**, 170–184.

Richardson, J.B. & Rasul, S.M. 1990. Palynofacies in a Late Silurian regressive sequence in the Welsh Borderland and Wales. *Journal of the Geological Society, London*, **147**, 675–686, http://doi.org/10.1144/gsjgs.147.4.0675

Rixton, A.E. (ed.) 1976. *Fossil Animals, Their Preparation and Conservation*. Athlone Press, London, 59–83.

Rogerson, C., Edwards, D., Axe, L. & Davies, K.L. 2002. A new embryophyte from the upper Silurian of Shropshire, England. *Special Papers in Palaeontology*, **67**, 233–250.

Savage, N.M. 1988. The use of sodium polytungstate for conodont separations. *Journal of Micropalaeontology*, **7**, 39–40, http://doi.org/10.1144/jm.7.1.39

Swift, A. & Martill, D.M. (eds). 1999. *Fossils of the Rhaetian Penarth Group*. Paleontological Association, London.

Appendix B. Fossil Database

Class			
Thelodont			
Fossil ID	**Binomial**	**Scale type**	**Stub box**
DBB5.500.1	*Paralogania ludlowiensis*	Trunk	DBB5 500µm
DBB4.500.4	*Paralogania ludlowiensis*	Trunk	DBB4 500µm
DBB4.500.3	*Paralogania ludlowiensis*	Trunk	DBB4 500µm
DBB4.500.5	*Paralogania ludlowiensis*	Trunk	DBB4 500µm
DBB6.500.1	*Paralogania ludlowiensis*	Trunk	DBB6 500µm
DBB4.500.2	*Paralogania ludlowiensis*	Trunk	DBB4 500µm
DBB20B.500.4	*Paralogania ludlowiensis*	Trunk	DBB20B 500µm
DBB20.500.1	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB.500.f	*Paralogania ludlowiensis*	Trunk	DBB 500µm
DBB20.500.28	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB5.500.8	*Paralogania ludlowiensis*	Trunk	DBB5 500µm
DBB20.500.16	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB20.500.22	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB5.500.1a	*Paralogania ludlowiensis*	Trunk	DBB5 500µm
DBB5.500.21	*Paralogania ludlowiensis*	Trunk	DBB5 500µm
DBB20.212.1	*Paralogania ludlowiensis*	Trunk	DBB20 212µm
DBB20.500.2	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB20.500.41	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB20.500.30	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB20.212.7	*Paralogania ludlowiensis*	Trunk	DBB20 212µm
DBB20.500.33	*Paralogania ludlowiensis*	Trunk	DBB20 500µm
DBB.500. j	*Paralogania ludlowiensis*	Trunk	DBB 500µm
DBB.500.v	*Paralogania ludlowiensis*	Trunk	DBB 500µm
DBB.500.z	*Paralogania ludlowiensis*	Trunk	DBB 500µm
DBB20B.212.2	*Paralogania ludlowiensis*	Trunk	DBB20B 212µm
DBB7.212.7	*Paralogania ludlowiensis*	Trunk	DBB7 212µm
DBB20B.212.3	*Paralogania ludlowiensis*	Trunk	DBB5 212µm
DBB5.212.10	*Paralogania ludlowiensis*	Trunk	DBB20B 212µm
DBB.212.au	*Paralogania ludlowiensis*	Trunk	DBB 212µm
DBB.212.bj	*Paralogania ludlowiensis*	Trunk	DBB 212µm
DBB5.212.2	*Paralogania ludlowiensis*	Trunk	DBB5 212µm
DBB5.212.1	*Paralogania ludlowiensis*	Trunk	DBB5 212µm
DBB.212.19	*Paralogania ludlowiensis*	Trunk	DBB 212µm
DBB.212.13	*Paralogania ludlowiensis*	Trunk	DBB 212µm
DBB.212.6	*Paralogania ludlowiensis*	Trunk	DBB 212µm
DBB18.212.2	*Paralogania ludlowiensis*	Trunk	DBB18 212µm
DBB4.212.1	cf.*Paralogania ludlowiensis*	Transitional	DBB4 212µm
DBB4.500.3	cf.*Paralogania ludlowiensis*	Transitional	DBB4 500µm
DBB.212.br	cf.*Paralogania ludlowiensis*	Transitional	DBB 212µm
DBB5.500.3	cf.*Paralogania ludlowiensis*	Transitional	DBB5 500µm
DBB20.500.23	cf.*Paralogania ludlowiensis*	Transitional	DBB20 500µm
DBB19.500.3	cf.*Paralogania ludlowiensis*	Transitional	DBB19 500µm
DBB.212.j	*Paralogania ludlowiensis*	Head	DBB 212µm
DBB.212.r	*Paralogania ludlowiensis*	Head	DBB 212µm
DBB.500.U	*Paralogania ludlowiensis*	Head	DBB 500µm
DBB.212.17	*Thelodus parvidens*	Trunk	DBB 212µm
DBB.212.2	*Thelodus parvidens*	Trunk	DBB 212µm
DBB5.212.4	*Thelodus parvidens*	Trunk	DBB5 212µm
DBB20.500.6	*Thelodus parvidens*	Trunk	DBB20 500µm
DBB.212.aq	*Thelodus parvidens*	Trunk	DBB 212µm

Class			
Acanthodian			
Fossil ID	**Binomial**	**Fossil Type**	**Stub box**
WQ2a.212.G	*Gomphonchus* sp	Scale	WQ2a 212µm
DBB20.500.40	*Gomphonchus* sp	Scale	DBB20 500µm
DBB4.212.1	*Nostolepis sp.*	Scale	DBB4 212µm
DBB5.500.h	*Nostolepis sp.*	indeterminate	DBB5 500µm
DBB5.212.1	Acanthodi Indet.	Scale	DBB5 212µm
WQ1b.G	Acanthodi Indet.	Fin spine	WQ1 212µm
WQ1a1.212.H	Acanthodi Indet.	Fin spine	WQ1 212µm
DBB20.500.2	Acanthodi Indet.	Fin spine	DBB20 500µm
DBB4.500.2a	Acanthodi Indet.	Fin spine	DBB4 500µm
DBB.212.q	Acanthodi Indet.	Fin spine	DBB 212µm
DBB5.500.1	Acanthodi Indet.	Fin spine	DBB5 500µm
DBB14.5.500.1	Acanthodi Indet.	Fin spine	DBB14.5 500µm
DBB19.500.5	Acanthodi Indet.	Tooth whorl	DBB19 500µm
WQ1a1.212.b	Acanthodi Indet.	Tooth whorl	WQ1a 212µm
DBBM 1	*Onchus murchisoni*	Fin spine	N/A
DBBM 2	*Onchus murchisoni*	Fin spine	N/A
DBBM 12-DBBM 13	Acanthodi Indet.	Fin spine	N/A

Class			
Bivalva			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBBM3	*Modiolopsis complanata*	Shell	N/A
Class			
Gastropoda			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBBM4	*Turbocheilus helicites*	Shell	N/A
DBBM5	*Turbocheilus helicites*	Shell	N/A
Class			
Brachiopoda			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBB5.500.4	*Tunisiglossa cornea*	Shell	DBB4 500µm
DBB20.500.2	*Tunisiglossa cornea*	Shell	DBB20 500µm
DBB5.500.2	*Tunisiglossa cornea*	Shell	DBB5 500µm
DBB5.212.3	*Tunisiglossa cornea*	Shell	DBB5 212µm
S212.z2	*Lingula missendenensis*	Shell	Selfrag 212µm
DBB19.500.2	*Lingula missendenensis*	Shell	DBB19 500µm
DBB19.500.2	*Lingula missendenensis*	Shell	DBB19 500µm
DBB20.500.4	*Lingula missendenensis*	Shell	DBB20 500µm
DBB20.500.5	*Lingula missendenensis*	Shell	DBB20 500µm
DBB20.500.1	*Lingula missendenensis*	Shell	DBB20 500µm
DBB7.212.1	*Lingula missendenensis*	Shell	DBB7 212µm
Class			
Ostracoda			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBBM9	*Leperditia sp.*	Shell	N/A
DBB20B.500.1	*Frostiella groenvalliana*	Shell	DBB20B 212µm
DBB7.500.1	*Frostiella groenvalliana*	Shell	DBB7 500µm
DBBM8 1	*Frostiella groenvalliana*	Shell	N/A
DBB18.500.1	Non-palaeocope	Shell	DBB18 500µm
DBB18.500.3	*Londinia arisaigensis*	Shell	DBB18 500µm
DBB18.500.2	*Londinia arisaigensis*	Shell	DBB18 500µm
DBB14.5 500 1	*Londinia arisaigensis*	Shell	DBB14.5 500µm
DBBM8 2	*Londinia arisaigensis*	Shell	N/A
DBB8M 3	*Londinia arisaigensis*	Shell	N/A
DBB8M 4	*Londinia arisaigensis*	Shell	N/A
DBB8M 5	*Londinia arisaigensis*	Shell	N/A
DBBM8 6	*Londinia arisaigensis*	Shell	N/A
Class			
Merostomata			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBBM6-DBBM7	Eurypterid indet.	Denticle	N/A

Class			
Plant			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBBI.1	Plant indet.	Cross section in thin section	N/A
DBB.53.b	*Cooksonia pertoni*	sporangia	DBB 53µm
DBB500.b	*Cooksonia pertoni*	sporangia	DBB 500µm
DBB500.c	*Cooksonia pertoni*	sporangia	DBB 500µm
DBB6.53.4	*Cooksonia pertoni*	sporangia	DBB6 53µm
DBB16.500.1	*Cooksonia pertoni*	sporangia	DBB16 500µm
DBB15.500.1	*Cooksonia pertoni*	sporangia	DBB15 500µm
DBB1.500.1	*Cooksonia pertoni*	sporangia	DBB1 500µm
DBB5.53.4	*Cooksonia pertoni*	sporangia	DBB5 53µm
DBB1.53	*Cooksonia pertoni*	sporangia	DBB1 53µm
DBB4.53.5	*Cooksonia pertoni*	sporangia	DBB4 53µm
DBB14.500.1	*Cooksonia pertoni*	Axe	DBB14 500µm
DBB3.53	*Cooksonia pertoni*	Axe	DBB3 53µm
DBB5.500.2	*Cooksonia pertoni*	Axe	DBB5 500µm
DBB. 53.1	*Cooksonia pertoni*	Axe	DBB5 53µm
DBB5.500.1	*Cooksonia pertoni*	Axe	DBB5 500µm
DBB6.53	*Cooksonia pertoni*	Axe	DBB6 53µm
DBB2.53.3	*Cooksonia pertoni*	Axe	DBB2 53µm
DBB5.500.2	*Hollandophyton colliculum*	Axe	DBB5 500µm
DBB9.500.1	*Hollandophyton colliculum*	Axe	DBB9 500µm
DBB2.53	*Hollandophyton colliculum*	Axe	DBB2 53µm
DBB8.500.1	*Hollandophyton colliculum*	Axe	DBB8 500µm
DBB.53.d	*Synorisporites downtonensis*	sporangia	DBB 53µm
DBB.500.a	*Prototaxites* sp	Indet.	DBB 500µm
DBB8.53	*Prototaxites* sp	Indet.	DBB 53µm
DBB20.500.1	*Pachytheca sphaerica*	Indet.	DBB20 500µm
Class			
Fungi and allies			
Fossil ID	**Binomial**	**Fossil type**	**Stub Box**
DBB7.53.3	*Nematothallus pseudo-vasculosa*	Cuticle	DBB7 53µm
DBB.53.I	*Nematothallus pseudo-vasculosa*	Cuticle	DBB 53µm
DBB6.53.11	*Nematothallus pseudo-vasculosa*	Cuticle	DBB6 53µm
DBB6.53.6	*Nematothallus pseudo-vasculosa*	Cuticle	DBB6 53µm
DBB2.500.41	*Nematothallus pseudo-vasculosa*	Cuticle	DBB2 500µm
DBB7.53	*Nematothallus pseudo-vasculosa*	Cuticle	DBB7 53µm
DBB5.53.3	*Nematothallus pseudo-vasculosa*	Cuticle	DBB5 53µm
DBB10a.53	Organic-walled indet.	Phytoclast	DBB10a 53µm
DBB2.500.11	Organic-walled indet.	Possilbe Fungal hyphae	DBB2 500µm
DBB13.500.1	Organic-walled indet.	Possilbe Fungal hyphae	DBB13 500µm
DBB3.53.7	Organic-walled indet.	Indet.	DBB3 53µm
DBB7.53.4	Organic-walled indet.	Indet.	DBB7 53µm
DBB4.53.6	Organic-walled indet.	Indet.	DBB4 53µm
DBB9.53	Organic-walled indet.	Indet.	DBB9 53µm
DBB7.53.7	Organic-walled indet.	Indet.	DBB7 53µm
DBB5.53	Organic-walled indet.	Indet.	DBB5 53µm
DBB21.53	Organic-walled indet.	Indet.	DBB2 53µm

Class		
Trace fossil		
Fossil ID	**Binomial**	**Stub box**
DBB1I	N/A	N/A
DBB2I	*Teichichnus sp. & Planolites sp.*	N/A
DBB3I	N/A	N/A
DBB4I	*Teichichnus sp. & Planolites sp.*	N/A
DBB5I	*Teichichnus sp. & Planolites sp.*	N/A
DBB6I	*Teichichnus sp.*	N/A
DBB7I	N/A	N/A
DBB8I	*Teichichnus sp. & Planolites sp.*	N/A
DBB9I	*Teichichnus sp. & Planolites sp.*	N/A
DBB11I	N/A	N/A
DBB12I	N/A	N/A
DBB13I	*Teichichnus sp.*	N/A
DBB14I	*Teichichnus sp.*	N/A
DBB15I	N/A	N/A
DBB16I	N/A	N/A
DBB17I	*Teichichnus sp.*	N/A
DBB18I	*Teichichnus sp. & Planolites sp.*	N/A
DBB19I	*Teichichnus sp. & Planolites sp.*	N/A
DBB2.53.1	Coprolite	DBB2 53µm
DBB14.53	Coprolite	DBB14 53µm
DBB4.53.3	Coprolite	DBB4 53µm

Appendix C. Conference Abstracts.

60th *Symposium of vertebrate palaeontology and comparative anatomy, Oxford, U.K. 2012. Poster presentation.*

The Palaeontology and Sedimentology of the Downton Bone Bed.

Luke M. Hauser

School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL. luke.hauser@port.ac.uk

As a component of this current research a section from the upper Silurian (Ludlow series) of the Welsh borderland is being documented. The locality contains a previously, very poorly documented bone bed. Previous studies of analogous bone beds have yielded fossil remains of jawless fish and early jawed vertebrates in addition to early plants and some of the first land animals (Arthropoda).
This research is part of IGCP 591 entitled the early to middle Paleozoic revolution. The aims of the research include a documentation of all of the macro- and micro-fauna and flora found in the section and sedimentological analysis to enable interpretation of the palaeoenvironment and palaeoecology of the locality during the late Silurian.

In order to process large amounts of the bone bed to extract the fossil content a sample was sent to a Swiss organization (SELFRAG) to see if a new technique using high voltage electric pulses could fragment the rock so that the microfossils can be extracted quickly and easily as a alternative to the time consuming methods that will be used otherwise. Once processed then scanning electron and light microscopy will be used to identify the fossils. The sedimentology will be studied by using hand specimens and thin sections.

Progress so far has involved curating the lithological specimens, a lithostratigraphically review, initial processing, lithological descriptions of the bone bed and its component horizons, and fieldwork to collect more samples, place the Downton Bone Bed in a stratigraphical context and determine and its lateral extent.

3rd IGCP 591 the early to middle Paleozoic revolution annual meeting, Lund, Sweden 2013. Poster presentation.

The Palaeontology and Sedimentology of the Downton Bone Bed.

Luke M. Hauser

School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL. luke.hauser@port.ac.uk

As a component of this current research a section from the upper Silurian (Ludlow Series) of the Welsh borderland is being documented. The locality contains a previously, very poorly documented bone bed. Previous studies of analogous bone beds have yielded fossil remains of jawless fish and early jawed vertebrates in addition to early plants and some of the first land animals (Arthropoda).

The aims of the research include a documentation of all of the macro- and micro-fauna and flora found in the section and sedimentological including palaeoichnological analysis to enable interpretation of the palaeoenvironment and palaeoecology of the locality during the late Silurian.

In order to process large amounts of the bone bed to extract the fossil content a sample was sent to a Swiss organization (SELFRAG) to see if a new technique using high voltage electric pulses could fragment the rock so that the microfossils could be extracted quickly and easily as an alternative to the time-consuming methods that are being used otherwise. Once processed then scanning electron and light microscopy are being used to identify the fossils. The sedimentology is being studied by using hand specimens and thin sections.

Progress so far has involved curating the lithological specimens, a lithostratigraphical review, initial processing, lithological descriptions of the bone bed and its component horizons, and fieldwork to collect more samples, placing the Downton Bone Bed in a stratigraphical context and determining its lateral extent.

4th IGCP 591 the early to middle Paleozoic revolution annual meeting, Tartu, Estonia 2014. Poster presentation.

Vertebrates of the Downton Bone Bed

Luke M. Hauser

University of Portsmouth, School of Earth & Environmental Sciences, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK. luke.hauser@port.ac.uk

The Downton Bone Bed (DBB), from the upper Silurian (Ludlow Series) of the Welsh borders, occurs within an interbedded siltstone and sandstone facies in the Platyschisma Shale Member of the Downton Castle Sandstone Formation. The term "bone bed" is misleading with respect to the Silurian as the bulk of the vertebrate material is in the form of denticles which histologically are more similar to teeth so perhaps "tooth bed" would be a more accurate term.

The extraction of the vertebrate material has been a considerable challenge as the rock lacks calcium carbonate cement; therefore most acids typically used in microvertebrate extraction have had no effect. Recently, a number of methods were used on a single piece of the DBB and resulted in the entire rock disaggregating, these methods included: mechanical fragmentation, immersion in paraffin, rapid freeze/thaw (in liquid nitrogen) and microwaving. The results of this have been much better than expected and the extracted material is well preserved.
The DBB contains some of the best preserved Silurian vertebrates in the UK. Unlike the Ludlow Bone Bed, which has mostly black material, the DBB's vertebrate remains are well preserved and light brown to tan in colour. This means that, potentially, the denticle histology can be studied.

The DBB vertebrate assemblage is made up primarily of the single thelodont species present: *Paralogania ludlowiensis*. There are also two genera of acanthodian: *Poracanthodes porosus* and *Nostolepis linleyensis*. This low diversity suggests that the "Downton Sea" was a restricted environment, which is in agreement with the sedimentological and the ichnological data from the section.

24th Symposium of palaeontological preparation and conservation with the geological curators' group, Southampton, U.K. 2015. Oral presentation.

Breaking bad…bone beds: processing the Downton Bone Bed

Luke M. Hauser

University of Portsmouth, School of Earth & Environmental Sciences, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK. luke.hauser@port.ac.uk

Bone beds have often been a focus for micropalaeontological study as the high concentration of fossil material allows vertebrate palaeontologists the returns normally experienced only by nannofossil workers and palynologists. It is not always straightforward to release the fossil material within bone beds and the extraction of microfossils from the Downton Bone Bed of the upper Silurian is particularly challenging. Outlined here is an integrated method for processing this bone bed using liquid paraffin and a microwave oven and a comparison in terms of quality and quantity with material recovered using other techniques. This method has also been used on other bone beds to test its effectiveness. This integrated method allows for the recovery of microvertebrates such as thelodonts, and also internal moulds of ostracodes, brachiopods and early plant material. This integrated method is enabling for the first time study of the Downton Bone Bed's fossil content.

63rd Symposium of vertebrate palaeontology and comparative anatomy, Southampton, U.K. 2015. Oral presentation.

The Downton "Tooth Bed": a lost world

Luke M. Hauser

University of Portsmouth, School of Earth & Environmental Sciences, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK. luke.hauser@port.ac.uk

The Downton Bone Bed is a vertebrate-rich (fish microremains) deposit from the middle Ludfordian (Ludlow Series) within the Downton Sandstone Formation (Platyschisma Shale Member). The Silurian bone beds of the Welsh borders have been well documented over the past 175 years, except the Downton Bone Bed which seems to have been largely overlooked. This is probably for a number of reasons but two of the most likely are 1) its proximity to the Ludlow Bone Bed and 2) the preservational colour of the denticles. The Downton Bone Bed contains not only vertebrates, but also a wide range of other fossils including bivalves, gastropods, ostracodes, arthropods, brachiopods and plants. This gives a snapshot into the Ludlow area during the late Silurian, a time of tremendous change, as the Downton Bone Bed was deposited on a near shore sand bar during the Lau Event, which is associated with the largest carbon isotope excursion in the Phanerozoic. Results suggest that the "Downton Sea" was a restricted environment indicated by the low diversity assemblages. The most common vertebrate in the Downton Bone Bed is the thelodont Paralogania ludlowiensis which makes up 81% of the total identified vertebrate fauna.

61st Palaeontological association annual meeting, Imperial college London, U.K. 2017. Oral presentation.

The Downton Bonebed: insights into a lost world.

Luke M. Hauser

University of Portsmouth, School of Earth & Environmental Sciences, Burnaby Building, Burnaby Road, Portsmouth, PO1 3QL, UK. luke.hauser@port.ac.uk

The Downton Bonebed is a multitaxic Fossil Concentration-Lagerstätte located in the Platyschisma Shale Member of the Downton Castle Sandstone Formation *c*. 1.5 m above the Ludlow Bonebed. The Downton Bonebed has received little direct study since its discovery over a century ago. The aims of this study were to catalogue for the first time the fossil contents of the Downton Bonebed, and to look at the sedimentology to define the depositional environment that the bonebed formed in, as well as its wider global context. The bonebed is rich in fossils with a broad diversity of vertebrates, invertebrates, plants and allies, however with each group the diversity is low suggesting that the Downton Bonebed was formed in a restricted environment. T*he sedimentology reveals evidence of two energy conditions shifting between quiet low energy setting with trace fossils present* and periods of rapid burial in which all of the other fossils are found associated with swaley and hummocky cross laminations suggesting large storms. The environmental setting for the Downton Bonebed is a quiet hyposaline inlet/lagoon in close proximity to a terrestrial freshwater source, cut off from the Downton Sea by a barrier or barrier beach. A-B *Paralogania ludlowiensis*, trunk scales. C *Paralogania ludlowiensis* head scale. D Acanthodian tooth whrol. E Acanthodian fragment of fin spine. F *Gomphonchus* sp. denticle. G-H *Londinia arisaigensis*? I *Lingula missendenensis.* J-K *Cooksonia pertoni* axes. L possible coprolite. M *Cooksonia pertoni* sporangia. O Terminal end of *Hollandophyton colliculum* axe. P Fragment of *Pachytheca* sp.

Appendix D. Ethical Review.

Dear Luke
You will need to complete the attached form and include within your thesis. I wasn't sure whether more was required so contacted the chair of the Science Faculty ethics committee, Jim House.
My message to him and his response are below. Note that he's suggesting that all that you need to do is complete the attached form, but what you must do is emphasize that collecting was undertaken responsibly and with permission (giving details).
David

Dear Jim
I have a part-time PhD student (Luke Hauser) due to submit his thesis this summer. I have looked at the UPR16 form and from this imagine that in addition to ticking the relevant boxes Luke simply needs to complete the section that explains why no ethical review was undertaken (i.e. that the project does not raise any ethical issues - other than the normal academic ones which are covered by tick-boxes on the form - in that he has been working on rocks and fossils, long dead and collected his rock samples with permission of the landowners).
Please can you confirm that this is the case (or if not, what now needs to be done).
David

Dear David, the intention, fairly soon, is for all research undertaken at UoP to undergo ethical review. For those that don't (or aren't likely to) raise any ethical issues there is new online ethics review system (although it remains a little clunky still) available from the UoP main ethics webpage. By answering a series of questions, you (or your student) will either be referred to make an application to the Faculty Ethics Committee, or as you say, get a favourable ethical opinion straight-away. The future intention is for this to be done before the research is undertaken, and all research such as your student's should sail-through without need to prepare applications and wait weeks for review. It also means Faculty Ethics Committees aren't continually reviewing proposals that have no ethical issues.

In your case it might simply be easier to complete the form as you say, giving the reasons why there are no ethical issues - I'd also mention in the form whether there were:

a. Risks of damage to physical and/or ecological environmental features?
b. Risks of damage to features of historical or cultural heritage (e.g. impacts of study techniques, taking of samples)?
Then you should be fine.

Our current UoP ethics advisor (Simon Kolstoe) essentially inherited the online ethics system (and is trying to make it work better, which is why it hasn't been fully adopted / enforced quite yet), and the UPR16 form was (I think) an attempt to reduce red faces at PhD vivas when external examiners discovered that research that should have had ethical review (e.g. human research) had been undertaken without such review - a problem that occasionally arose a few years ago.
Please come back to me if still unsure.
Kind regards,

Jim

FORM UPR16

Research Ethics Review Checklist

Please include this completed form as an appendix to your thesis (see the Postgraduate Research Student Handbook for more information

Postgraduate Research Student (PGRS) Information				**Student ID:**	417218
PGRS Name:	Luke Matthew Hauser				
Department:	SEES	**First Supervisor:**	Dr David K. Loydell		
Start Date: (or progression date for Prof Doc students)		**October 2011**			
Study Mode and Route:	Part-time ☒ Full-time ☐	MPhil ☐ PhD ☒	MD ☐ Professional Doctorate ☐		

Title of Thesis:	The palaeontology and sedimentology of the upper Silurian Downton Bone Bed of Weir Quarry, near Ludlow, England
Thesis Word Count: (excluding ancillary data)	26,197

If you are unsure about any of the following, please contact the local representative on your Faculty Ethics Committee for advice. Please note that it is your responsibility to follow the University's Ethics Policy and any relevant University, academic or professional guidelines in the conduct of your study

Although the Ethics Committee may have given your study a favourable opinion, the final responsibility for the ethical conduct of this work lies with the researcher(s).

UKRIO Finished Research Checklist:
(If you would like to know more about the checklist, please see your Faculty or Departmental Ethics Committee rep or see the online version of the full checklist at: http://www.ukrio.org/what-we-do/code-of-practice-for-research/)

a) Have all of your research and findings been reported accurately, honestly and within a reasonable time frame?	YES ☒ NO ☐
b) Have all contributions to knowledge been acknowledged?	YES ☒ NO ☐
c) Have you complied with all agreements relating to intellectual property, publication and authorship?	YES ☒ NO ☐
d) Has your research data been retained in a secure and accessible form and will it remain so for the required duration?	YES ☒ NO ☐
e) Does your research comply with all legal, ethical, and contractual requirements?	YES ☒ NO ☐

Candidate Statement:

I have considered the ethical dimensions of the above named research project, and have successfully obtained the necessary ethical approval(s)

Ethical review number(s) from Faculty Ethics Committee (or from NRES/SCREC):	

If you have *not* submitted your work for ethical review, and/or you have answered 'No' to one or more of questions a) to e), please explain below why this is so:

This research has not been submitted for ethical review because it was conducted on geological samples which are exempt from ethical considerations.All samples were collected responsibly and with permission from the land owerners (Natural England).

Signed *(PGRS)*:		**Date:** 07/08/2017

References

Abbott, G. D., Ewbank, G., Edwards, D., & Wang, G. Y. (1998). Molecular characterization of some enigmatic Lower Devonian fossils. *Geochimica et Cosmochimica Acta*, *62*(8), 1407-1418.

Agassiz, J. L. R. (1837). *Recherches sur les Poissons fossiles, Tome III. Contenant l'Histoire de l'ordre des Placoides*. Petitpierre, Neuchâtel et Soleure, Switzerland.

Agassiz, J. L. R. (1838). In Murchison, R.J., On the fishes of the Upper Ludlow rock or upper beds of the Silurian System. *Report of the British Association for the Advancement of Science*, Liverpool, *6*(91).

Agassiz, J. L. R. (1839). On the fishes of the Upper Ludlow rock. In Murchison, R.J., *The Silurian System, Pt, 1*, 605-607.

Ainsworth, R. B., Richardson, J., & Rasul, S. (1991). Discussion on palynofacies in a Late Silurian regressive sequence on the Welsh Borderland and Wales; *Journal of the Geological Society*, *148*, 781-784.

Aldridge, R. J. (1975). The stratigraphic distribution of conodonts in the British Silurian. *Journal of the Geological Society*, *131*(6), 607-618.

Allard, H., Carpenter, S. C., Duffin, C. J., & Benton, M. J. (2015). Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). *Proceedings of the Geologists' Association*, *126*(6), 762-776.

Allen, J. R. L. (1985). *Principles of Physical sedimentology*. Allen & Unwin. pp. 272

Allen, J. R. L. (1974). The Devonian rocks of Wales and the Welsh Borderland. In Owen, T.R. (eds.) *The Upper Palaeozoic and Post-Palaeozoic rocks of Wales*. 47-84.

Allen, J. R. L., & Richardson, J. B. (1985). Marine to fresh water: the sedimentology of the interrupted environmental transition (Ludlow-Siegenian) in the Anglo-Welsh region: discussion. *Philosophical Transactions of the Royal Society of London Series B, 309*, 104.

Allen, J. R. L., & Tarlo, L. B. (1963). The Downtonian and Dittonian facies of the Welsh borderland. *Geological Magazine*, *100*(2), 129-155

Allison, P. A. (1991). Taphonomy of non-mineralized tissues: in Allison, P.A., and Briggs, D.E.G, (eds.), *Taphonomy: Releasing the data locked in the fossil record*.

Allulee, J. L., & Holland, S. M. (2005). The sequence stratigraphic and environmental context of primitive vertebrates: Harding Sandstone, Upper Ordovician, Colorado, USA. *Palaios*, *20*(6), 518-533.

Anderton, R., Bridges P. H, Leeder, M. R. & Sellwood, B. W. (1979). *A dynamic stratigraphy of the British Isles.* George Allen & Unwin, London.

Andrew, K. (2009). Gap fills for geological specimens–or making gap fills with Paraloid. *NatSCA News*, *16*, 41-45.

Antia, D. D. (1979a). Comments on the environments and faunas across the Ludlovian-Downtonian boundary (upper Silurian) at Siefton, Salop. *Geological Journal*, *14*(1), 127-134.

Antia, D. D. (1979b). Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering, and microbiotas. *Mercian Geologist*, *7*(2) 93-174.

Antia, D. D. J. (1980). Sedimentology of the type section of the upper Silurian Ludlow-Downton Series boundary at Ludlow, Salop, England. *Mercian Geologist*, *7*, 291-321.

Antia, D. D. J. (1981). The Temeside Bone-Bed and associated sediments from Wales and the Welsh Borderland. *Mercian Geologist*, *8*(3), 163-215.

Antia, D. D. J., & Whitaker, J. H. McD. (1978). A scanning electron microscope study of the genesis of the upper Silurian Ludlow Bone Bed. In Whalley, W.B. (eds.) *Scanning electron microscopy in the study of sediments.* Geo Abstracts, Norwich, pp. 119-136.

Arthur, M. A., Williams, D. F., & Jones, D. S. (1983). Seasonal temperature-salinity changes and thermocline development in the mid-Atlantic Bight as recorded by the isotopic composition of bivalves. *Geology*, *11*(11), 655-659.

Aslan, A., & Behrensmeyer, A. K. (1996). Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. *Palaios*, *11*(5) 411-421.

Baarli, B. G. Johnson, ME, Antoshkina, AI, (2003). Silurian stratigraphy and paleogeography of Baltica. *New York State Museum Bulletin, 493,* 3-34.

Badgley, C. (1986). Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology*, *12*(2), 119-142.

Badgley, C., Bartels, W. S., Morgan, M. E., Behrensmeyer, A. K., & Raza, S. M. (1995). Taphonomy of vertebrate assemblages from the Paleogene of northwestern Wyoming and the Neogene of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *115*(1-4), 157-180.

Barber, C. A. (1889). The structure of Pachytheca. *Annals of Botany*, *3*(10), 141-148.

Barber, C. A. (1891). The structure of Pachytheca. II. *Annals of Botany*, *5*(18), 145-162.

Barton, D. G., & Wilson, M. V. (2005). Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10 000 years of environmental change. *Canadian Journal of Earth Sciences*, *42*(2), 137-149.

Bassett, M. G. (1986). Brachiopodes inarticules. In Racheboeuf P.R. (ed.) *Le Groupe Lievin, Pridoli– Lochkovien de l'Artois (N. France). Biostratigraphie du Paléozoique, 3,* 85-97.

Bassett, M. G., Bluck, B. J., Cave, R., Holland, C. H., & Lawson, J. D. (1992). Silurian. In Cope, J. C. W. Ingham, J. K. and Rawson, P. F. (eds.) Atlas of palaeogeography and lithofacies. *Geological Society, London, Memoirs*, *13*(1), 17-56.

Bassett, M. G. & Lawson, J. Autecology of Silurian organisms. *Special Papers in Palaeontology*, *32*.

Bassett, M. G., Lawson, J. D., & White, D. E. (1982). The Downton Series as the fourth series of the Silurian System. *Lethaia*, *15*(1), 1-24.

Behrensmeyer, A. K. (1975). The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rodolf, Kenya. *Bulletin of the Museum of Comparative Zoology*, *146*, 473–578.

Behrensmeyer, A. K. (1982). Time resolution in fluvial vertebrate assemblages. *Paleobiology*, *8*(3), 211-227.

Behrensmeyer, A. K. (1987). Miocene fluvial facies and vertebrate taphonomy in northern Pakistan. Pp. 169–176 In Recent developments in fluvial sedimentology. Special publication 39. F. G. Ethridge, R.M. Flores, and M.D. Harvey, (eds.) *Society of Economic Paleontology and Mineralogy*.

Behrensmeyer, A. K. (1988). Vertebrate preservation in fluvial channels. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *63*(1-3), 183-199.

Behrensmeyer, A. K. (1991). Terrestrial vertebrate accumulations. *Taphonomy: releasing the data locked in the fossil record*, *9*, 291-335.

Behrensmeyer, A. K., & Chapman, R. (1993). Models and simulations of time-averaging in terrestrial vertebrate accumulations: in Kidwell. S.M., *and Behrensmeyer,* A.K., (eds.) *Taphonomic Approaches to Time Resolution in Fossil Assemblages: Short Courses in Paleontology*, (6), 125-149.

Behrensmeyer, A. K., & Hill, A. P. (Eds.). (1988). *Fossils in the making: vertebrate taphonomy and paleoecology* (No. 69). University of Chicago Press.

Behrensmeyer, A. K., & Hook, R. W. (1992). Paleoenvironmental contexts and taphonomic modes. In (A. K. Behrensmeyer, JD Damuth, WA DiMichele, R. Potts, HD Sues & SL Wing, Eds) *Terrestrial ecosystems through time*. University of Chicago Press Chicago, *324*, 416.

Behrensmeyer, A. K., Kidwell, S. M., & Gastaldo, R. A. (2000). Taphonomy and paleobiology. *Paleobiology*, *26*(S4), 103-147.

Behrensmeyer, A. K., Rogers, R. R., Eberth, D. A., & Fiorillo, A. R. (2007). Bonebeds through time. *Bonebeds: Genesis, analysis, and paleobiological significance*, 65-101.

Beiner, G. G., & Rabinovich, R. (2013). An elephant task—conservation of elephant remains from Revadim Quarry, Israel. *Journal of the Institute of Conservation*, *36*(1), 53-64.

Berg, D. P. (1940). Classification of fishes, both recent and fossil. *Transactions of the Institute of Zoology, Academy of Science USSR*, *5*, 87-517.

Berman, D. S. (1976). Occurrence of Gnathorhiza (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species. *Journal of Paleontology*, 1034-1039.

Best, M. M., & Kidwell, S. M. (2000). Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings. II. Effect of bivalve life habits and shell types. *Paleobiology*, *26*(1), 103-115.

Betancourt, J. L., Van Devender, T. R., & Martin, P. S. (Eds.). (1990). *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press.

Bianucci, G., Di Celma, C., Collareta, A., Landini, W., Post, K., Tinelli, C., & Malinverno, E. (2016). Fossil marine vertebrates of Cerro Los Quesos: Distribution of cetaceans, seals, crocodiles, seabirds, sharks, and bony fish in a late Miocene locality of the Pisco Basin, Peru. *Journal of Maps*, *12*(5), 1037-1046.

Blieck, A., Cuvelier, J., & Thierry, O. (2013). Eurypterides des collections de Paleontologie de Lille: collections du Musée d'histoire naturelle de Lille (vii) et collections de l' Université Lille 1 (catalogue I).

Blob, R. W. (1997). Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates. *Palaios*, 12, 151-164.

Blondel, C. (1992). Initiation à la micropalaeo-ichthyologie des micro-restes des vertebrés du Ludlow Bone Bed (Silurian superieur, Angleterre). *Memoire de Maitrise de Géologie Fondamentale et Applique*. Université des Sciences et Technologies de Lille, Flandres, Artois.

Boucot, A. J. (1975). Standing diversity of fossil groups in successive intervals of geologic time viewed in the light of changing levels of provincialism. *Journal of Paleontology*, *49*(6) 1105-1111.

Boyce, C. K., Hotton, C. L., Fogel, M. L., Cody, G. D., Hazen, R. M., Knoll, A. H., & Hueber, F. M. (2007). Devonian landscape heterogeneity recorded by a giant fungus. *Geology*, *35*(5), 399-402.

Bradfield, K. E., & Tucker, E. V. (1986). A section in Linley Brook (Shropshire) showing a previously unrecorded junction between the Ludlow and Přídolí Series. *Geological Journal*, *21*(4), 375-380.

Bradfield, K.E.S., (1999). *Fossil communities of the late Ludlow and early Pridoli in Wales and the Welsh Borderland*, in Boucot, A.J., and Lawson, J.D., (eds.), *Paleocommunities: A Case Study from the Silurian and early Devonian*, Cambridge, UK, Cambridge University Press. pp. 370-372.

Brain, C. K. (1980). Some criteria for the recognition of bone-collecting agencies in African caves. In (Behrensmeyer, AK, & Hill, AP, (eds.) *Fossils in the making*.

Brain, C. K. (1983). *The hunters or the hunted? An introduction to African cave taphonomy*. University of Chicago Press.

Brand, L. R., Esperante, R., Chadwick, A. V., Porras, O. P., & Alomía, M. (2004). Fossil whale preservation implies high diatom accumulation rate in the Miocene–Pliocene Pisco Formation of Peru. *Geology*, *32*(2), 165-168.

Brandt, D. S. (1989). Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology. *Palaios*, *4*(4) 303-309.

Brazeau, M. D. (2012). A revision of the anatomy of the Early Devonian jawed vertebrate Ptomacanthus anglicus Miles. *Palaeontology*, *55*(2), 355-367.

Brigaud, B., Pucéat, E., Pellenard, P., Vincent, B., & Joachimski, M. M. (2008). Climatic fluctuations and seasonality during the Late Jurassic (Oxfordian–Early Kimmeridgian) inferred from δ18O of Paris Basin oyster shells. *Earth and Planetary Science Letters*, *273*(1-2), 58-67.

Bremer, O. (2017). *Silurian vertebrates of Gotland (Sweden) and the Baltic Basin* (Doctoral dissertation, Acta Universitatis Upsaliensis).

Brenchley, P. J., & Harper, D. (1998). *Palaeoecology: ecosystems, environments and evolution*. CRC Press.

Brenchley, P. J., Marshall, J. D., Carden, G. A. F., Robertson, D. B. R., Long, D. G. F., Meidla, T., Hints, L. & Anderson, T. F. (1994). Bathymetric and isotopic evidence for a short-lived Late Ordovician glaciation in a greenhouse period. *Geology*, *22*(4), 295-298.

Brett, C. E. (1990). Obrution deposits. *Palaeobiology: a synthesis. Blackwell Scientific, London*, 239-243.

Brett, C. E., & Walker, S. E. (2002). Predators and predation in Paleozoic marine environments. *The Paleontological Society Papers*, *8*, 93-118.

Broad, D. S. (1972). *Upper Silurian and Lower Devonian Heterostraci from Yukon and Northwest Territories, Canada*. (Doctoral dissertation, University of Bristol).

Broad, D. S., & Dineley, D. L. (1973). *Torpedaspis*, a new Upper Silurian and Lower Devonian genus of Cyathaspididae (Ostracodermi) from Arctic Canada. *Bulletin of the Geological Survey of Canada*, *222*, 53-90.

Broad, D. S., Dineley, D. L., & Miall, A. D. (1968). The Peel Sound Formation (Devonian) of Prince of Wales and adjacent islands: A preliminary report. *Arctic*, *21*, 84-91.

Brodie, P. B. (1869). On the occurrence of remains of *Eurypterus* and *Pterygotus* in the Upper Silurian rocks in Herefordshire. *Quarterly Journal of the Geological Society*, *25*(1-2), 235-237.

Brongersma-Sanders, M. (1957). Mass mortality in the sea. *Geological Society of America Memoirs*, *67*, 941-1010.

Brotzen, F. (1934). Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fishresten. *Zeitschrift für Geschiebeforschung*. *10*, 1-66.

Brown, B. (1935). Sinclair dinosaur expedition, 1934. *Natural History*, *36*(1), 2-15.

Bruguière J.G. (1797). *Tableau Encyclopédique et Méthodique des trois Règnes de la Nature: vers, coquilles, mollusques et polypes divers*. Panckoucke, Paris. *2*, 190-286.

Bruton, D. L. (2001). A death assemblage of priapulid worms from the Middle Cambrian Burgess Shale. *Lethaia*, *34*(2), 163-167.

Buatois, L. A., & Mángano, M. G. (2011). *Ichnology: organism-substrate interactions in space and time*. New York, Cambridge University Press.

Buatois, L. A., Gingras, M. K., MacEachern, J., Mángano, M. G., Zonneveld, J. P., Pemberton, S. G., R. G., Netto & Martin, A. (2005). Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios*, *20*(4), 321-347.

Buckland, W. (1829). XII.—On the Discovery of Coprolites, or Fossil Fæces, in the Lias at Lyme Regis, and in other Formations. *Transactions of the Geological Society of London*, *2*(1), 223-236.

Burmeister, H. (1843). *Die Organisation der Trilobiten, aus ihren lebenden Verwandten entwickelt; nebst systematischen Uebersicht aller zeither beschriben Arten*. G. Reimer, Berlin, 148. 1-148.

Burnett, W. C. (1977). Geochemistry and origin of phosphorite deposits from off Peru and Chile. *Geological Society of America Bulletin*, *88*(6), 813-823.

Burrow, C. J. (2003). Earliest Devonian gnathostome microremains from central New South Wales (Australia). *Geodiversitas*, *25*(2), 273-288.

Burrow, C. J. (2011). A partial articulated acanthodian from the Silurian of New Brunswick, Canada. *Canadian Journal of Earth Sciences*, *48*(9), 1329-1341.

Burrow, C. J. (2013). Reassessment of *Ischnacanthus*? *scheii* Spjeldnaes (Acanthodii, Ischnacanthiformes) from the latest Silurian or earliest Devonian of Ellesmere Island, arctic Canada. *Canadian Journal of Earth Sciences*, *50*(9), 945-954.

Burrow, C.J, den Blaauwen, J., Newman, M., & Davidson, R. (2016). The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica*, *19*(1), 1-83.

Burrow, C. J., & Simpson, A. J. (1995). A new ischnacanthid acanthodian from the Late Silurian (Ludlow, *ploeckensis* Zone) Jack Formation, north Queensland. *Memoirs of the Queensland Museum*, *38*, 383-396.

Burrow, C. J., & Turner, S. (2012). Fish stew: fossil fish taphonomy and the contribution of microfossils to documenting Devonian vertebrate history. *Global biodiversity, extinction intervals and biogeographic perturbations through time. Edited by J. Talent. Springer, Berlin, Germany*.

Burrow, C. J., Turner, S., Nowlan, G. S., & Denison, R. H. (2013). Vertebrate microremains from the Late Silurian of Arisaig, Nova Scotia, Canada. *Journal of Paleontology*, *87*(6), 1041-1059.

Burrow, C. J., Turner, S., Trinajstic, K., & Young, G. C. (2019). Late Silurian vertebrate microfossils from the Carnarvon Basin, Western Australia. *Alcheringa: An Australasian Journal of Palaeontology*, *43*(2) 1-16.

Burrow, C. J., Turner, S., & Young, G. C. (2010). Middle Palaeozoic microvertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld*, *19*(1-2), 37-54.

Burst, J. F. (1965). Subaqueously formed shrinkage cracks in clay. *Journal of Sedimentary Research*, *35*(2), 348-353.

Butler, R. J., & Barrett, P. M. (2008). Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. *Naturwissenschaften*, *95*(11), 1027-1032.

Buttler, C., & Stooshnov, A. (2002). The conservation of a Jurassic ichthyosaur. *The Conservator*, *26*(1), 24-31.

Calner, M. (2005). A Late Silurian extinction event and anachronistic period. *Geology*, *33*(4), 305-308.

Calner, M. (2008). Silurian global events–at the tipping point of climate change. In *Mass extinction* (pp. 21-57). Springer, Berlin, Heidelberg.

Calner, M., & Eriksson, M. J. (2006). Evidence for rapid environmental changes in low latitudes during the Late Silurian Lau Event: the Burgen-1 drillcore, Gotland, Sweden. *Geological Magazine*, *143*(1), 15-24.

Carruthers, W. (1872). On the history, histological structure, and affinities of *Nematophycus logani* Carr. (*Prototaxites logani* Dawson), an alga of Devonian age. *Monthly Microscopical Journal*, *8,* 160–172.

Case, E. C. (1935). Description of a collection of associated skeletons of *Trimerorhachis*. *Contributions from the Museum of paleontology University of Michigan*, *4*(13), 227-274

Castro, J. I. (2010). *The sharks of North America*. New York, Oxford University Press.

Cavin, L., Tong, H., Boudad, L., Meister, C., Piuz, A., Tabouelle, J., & Hua, S. (2010). Vertebrate assemblages from the early Late Cretaceous of southeastern Morocco: an overview. *Journal of African Earth Sciences*, *57*(5), 391-412.

Challinor, J. (1967). *A dictionary of geology*. New York, Oxford University Press. 3rd ed.

Cherns, L. (1979). The environmental significance of *Lingula* in the Ludlow Series of the Welsh Borderland and Wales. *Lethaia*, *12*(1), 35-46.

Cherns, L., Cocks, L. R. M., Davies, J. R., Hillier, R. D., Waters, R. A., & Williams, M. (2006). Silurian: the influence of extensional tectonics and sea-level changes on sedimentation in the Welsh Basin and on the Midland Platform. *The geology of England and Wales*, 75-102.

Chiappe, L. M., Coria, R. A., Dingus, L., Jackson, F., Chinsamy, A., & Fox, M. (1998). Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature*, *396*(6708), 258.

Choo, B., Zhu, M., Qu, Q., Yu, X., Jia, L., & Zhao, W. (2017). A new osteichthyan from the late Silurian of Yunnan, China. *PloS one*, *12*(3), e0170929.

Choo, B., Zhu, M., Zhao, W., Jia, L., & Zhu, Y. A. (2014). The largest Silurian vertebrate and its palaeoecological implications. *Scientific Reports*, *4*, 5242.

Cocks, L. R. M., & Davidson, T. (1978). A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Palaeontographical Society Monograph*. *131*(549), 1–256.

Cocks, L. R. M., & Popov, L. E. (2009). Generic homes for British Silurian linguloid brachiopods. *Palaeontology*, *52*(2), 349-367.

Cohen, K. M., Finney, S. C., Gibbard, P. L., & Fan, J. X. (2013). The ICS international chronostratigraphic chart. *Episodes*, *36*(3), 199-204.

Colombi, C. E., Martinez, R. N., Correa, G., Fernández, E., Santi Malnis, P., Praderio, A. & Aguilar-Cameo, A. (2015). First Argentine microfossil bonebed from the Upper Triassic Marayes—El Carrizal Basin, San Juan Province. *Palaios*, *30*(10), 743-757.

Conkin, J. E., Conkin, B. M., & Lipchinsky, Z. L. (1976). *Middle Devonian (Hamiltonian) stratigraphy and bone beds on the east side of the Cincinnati Arch in Kentucky* (Vol. 1). University of Louisville Reproduction Services.

Conkin, J. E., Conkin, B. M., & Dasari, M. R. (1999). Sequential disconformities in the Devonian succession of southern Indiana and northwestern Kentucky. *American Association of Petroleum Geologists Bulletin*, *83*, 1367.

Conrad, T. A. (1838). Report on the palaeontological department of the survey. *New York Geological Survey, Annual Report*, *2*, 107-119.

Cook, E. (1995). Taphonomy of two non-marine Lower Cretaceous bone accumulations from southeastern England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *116*(3-4), 263-270.

Copeland, M. J. (1964). Stratigraphic distribution of Upper Silurian Ostracoda, Stonehouse Formation, Nova Scotia. *Bulletin of the Geological Survey of Canada*, *117*, 1-13.

Coram, R. A., Radley, J. D., & Martill, D. M. (2017). A Cretaceous calamity? The Hypsilophodon Bed of the Isle of Wight, southern England. *Geology Today*, *33*(2), 66-70.

Corsin, P. (1945). Les algues de l'Eodevonien de Vimy. *Sociétes des Sciences, de l'Agriculture et des Arts de Lille, Memoires*, *9*, 1-86.

Cramer, B. D., & Saltzman, M. R. (2005). Sequestration of ^{12}C in the deep ocean during the early Wenlock (Silurian) positive carbon isotope excursion. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *219*(3-4), 333-349.

Cramer, B. D., Schmitz, M. D., Huff, W. D., & Bergström, S. M. (2015). High-precision U–Pb zircon age constraints on the duration of rapid biogeochemical events during the Ludlow Epoch (Silurian Period). *Journal of the Geological Society*, *172*(2), 157-160.

Crippa, G., Angiolini, L., Bottini, C., Erba, E., Felletti, F., Frigerio, C., Frigerio J.A.I., Hennissen M.J., Leng M.R., Petrizzo I.,Raffi G., Raineri & M.H. Stephenson. (2016). Seasonality fluctuations recorded in fossil bivalves during the early Pleistocene: Implications for climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *446*, 234-251.

Cumbaa, S. L., Underwood, C. J., Schröder-Adams, C. J., & Arratia, G. (2013). Paleoenvironments and paleoecology of the vertebrate fauna from a Late Cretaceous marine bonebed, Canada. *Mesozoic Fishes*, 509-524.

Cuvier, G. (1795). Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Journal des Sciences, des Lettres et des Arts*, *2*, 433-449.

Cuvier, G. (1798). *Tableau élémentaire de l'histoire naturelle des animaux*. Baudouin.

Dalingwater, J. E. (1973). The cuticle of a eurypterid. *Lethaia*, *6*(2), 179-185.

Dalquest, W. W., & Mamay, S. H. (1963). A remarkable concentration of Permian amphibian remains in Haskell County, Texas. *The Journal of Geology*, *71*(5), 641-644.

Davidson, T. (1866). A monograph of the British fossil Brachiopoda. The Silurian Brachiopoda. *Palaeontographical Society Monograph, 7* (1), 1-4.

Dawson, J. W. (1859). On fossil plants from the Devonian rocks of Canada. *Quarterly Journal of the Geological Society*, *15*(1-2), 477-488.

Deang, J. F., Persons, A. K., Oppedal, A. L., Rhee, H., Moser, R. D., & Horstemeyer, M. F. (2018). Structure, property, and function of sheepshead (*Archosargus probatocephalus*) teeth. *Archives of Oral Biology*, *89*, 1-8.

De Koninck, L. G. (1881). Faune du calcaire carbonifère de la Belgique. Troisième partie, Gastéropodes. In *Annales du Musée royal d'Histoire naturelle de Belgique, série paléontologique 6*.

DeMaggio, A. E., & Stetler, D. A. (1980). Storage products in spores of *Onoclea sensibilis* L. *American Journal of Botany*, *67*(4), 452-455.

Denison, R. H. (1956). A review of the habitat of the earliest vertebrates *11*(8) *Fieldiana*: *Geology*, *11*, 357-457.

Denison, R. H. (1974). The structure and evolution of teeth in lungfishes. *Fieldiana: Geology*, *33*, 31-58.

Denison, R. H. (1979). *Acanthodii. Handbook of paleoichthyology, Part 5*. Edited by H-P. Schultze. Gustav Fischer Verlag, Stuttgart. New York, 62 pp.

Dearden, R. 2015. Fossil focus: Acanthodians. *Palaeontology Online*, *5*(10) 1-12.

Díaz-Martínez, E., & Grahn, Y. (2007). Early Silurian glaciation along the western margin of Gondwana (Peru, Bolivia and northern Argentina): Palaeogeographic and geodynamic setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *245*(1-2), 62-81.

Dineley, D. L. (1951). The northern part of the Lower Old Red Sandstone outcrop of the Welsh Borderland. *Transactions of the Woolhope Naturalists Field Club*, *14*, 127-147.

Dineley, D. L., & Metcalf, S. J. (1999). *Fossil Fishes of Great Britain* (Vol. 16). Joint Nature Conservation Committee.

Dixon E.E.L. (1921). *The geology of the South Wales coalfield—Part XIII*: *The country around Pembroke and Tenby*. Memoir of the Geological Survey of England and Wales.

Dodson, P. (1973). The significance of small bones in paleoecological interpretation. *Rocky Mountain Geology*, *12*(1), 15-19.

Dodson, P., & Wexlar, D. (1979). Taphonomic investigations of owl pellets. *Paleobiology*, *5*(3), 275-284.

Donato, S. V., Reinhardt, E. G., Boyce, J. I., Rothaus, R., & Vosmer, T. (2008). Identifying tsunami deposits using bivalve shell taphonomy. *Geology*, *36*(3), 199-202.

Donoghue, P. C., & Smith, M. P. (2001). The anatomy of *Turinia pagei* (Powrie), and the phylogenetic status of the Thelodonti. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *92*(1), 15-37.

Dorlodot, H. de. (1912). Le système Dévonien et sa limite inférieure. *Annales de la Société Géologique de Belgique*. 39, 291–371

Downs, J. P., Daeschler, E. B., Garcia, V. E., & Shubin, N. H. (2016). A new large-bodied species of *Bothriolepis* (Antiarchi) from the Upper Devonian of Ellesmere Island, Nunavut, Canada. *Journal of Vertebrate Paleontology*, *36*(6), e1221833.

Droser, M. L., & Bottjer, D. J. (1989). Ichnofabric of sandstones deposited in high-energy nearshore environments: measurement and utilization. *Palaios*, *4*(6) 598-604.

Dudley, J. P., Gibson, D. S. C., Haynes, G., & Klimowicz, J. (2001). Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, *39*(2), 187-194.

Dumas, S., and Arnott, R. W. C. (2006). Origin of hummocky and swaley cross-stratification, the controlling influence of unidirectional current strength and aggradation rate. *Geology*, *34*(12), 1073-1076.

Dunlop, J. A. (1996). A trigonotarbid arachnid from the Upper Silurian of Shropshire. *Palaeontology*, *39*(3), 605-614.

Dunlop, J. A. (1999). A replacement name for the trigonotarbid arachnid *Eotarbus* Dunlop. *Palaeontology*, *42*(1), 191-191.

Earp, J. R. (1938). The higher Silurian rocks of the Kerry district, Montgomeryshire. *Quarterly Journal of the Geological Society*, *94*(1-4), 125-160.

Eberth, D. A. (1990). Stratigraphy and sedimentology of vertebrate microfossil sites in the uppermost Judith River Formation (Campanian), Dinosaur Provincial Park, Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *78*(1-2), 1-36.

Eberth, D. A., & Ryan, M. (1992). Stratigraphy, depositional environments and palaeontology of the Judith River and Horseshoe Canyon formations (Upper Cretaceous) South Alberta, Canada. In *Abstracts AAPG/SEPM Annual Meeting, Calgary 1*, 107.

Eberth, D. A., Shannon, M., & Noland, B. G. (2007). A bonebeds database: classification, biases, and patterns of occurrence. *Bonebeds: Genesis, Analysis, and Paleobiological Significance: University of Chicago Press, Chicago*, 103-219.

Edwards, D. (1970). Fertile Rhyniophytina from the Lower Devonian of Britain. *Palaeontology*, *13*(3), 451-461.

Edwards, D. (1979). A late Silurian flora from the Lower Old Red Sandstone of south-west Dyfed. *Palaeontology*, *22*(1), 23-52.

Edwards, D., Axe, L., & Honegger, R. (2013). Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: *Nematothallus* revisited. *Botanical Journal of the Linnean Society*, *173*(4), 505-534.

Edwards, D., Bassett, M. G., & Rogerson, E. C. W. (1979). The earliest vascular land plants: continuing the search for proof. *Lethaia, 12*(4), 313-324.

Edwards, D., & Davies, E. C. (1976). Oldest recorded in situ tracheids. *Nature, 263*(5577), 494-495.

Edwards, D., Davies, K. L., & Axe, L. (1992). A vascular conducting strand in the early land plant *Cooksonia*. *Nature, 357*(6380), 683-685.

Edwards, D., Davies, K. L., Richardson, J. B., & Axe, L. (1995). The ultrastructure of spores of *Cooksonia pertoni*. *Palaeontology, 38*(1), 153-168.

Edwards, D., Davies, K. L., Richardson, J. B., Wellman, C. H., & Axe, L. (1996). Ultrastructure of *Synorisporites downtonensis* and *Retusotriletes* cf. *coronadus* in spore masses from the Přídolí of the Welsh Borderland. *Palaeontology, 39*(3), 783-800.

Edwards, D., & Feehan, J. (1980). Records of *Cooksonia*-type sporangia from late Wenlock strata in Ireland. *Nature, 287*(5777), 41-42.

Edwards, D., & Rogerson, E. C. W. (1979). New records of fertile Rhyniophytina from the late Silurian of Wales. *Geological Magazine, 116*(2), 93-98.

Edwards, D., & Richardson, J. B. (2004). Silurian and Lower Devonian plant assemblages from the Anglo-Welsh Basin: a palaeobotanical and palynological synthesis. *Geological Journal, 39*(3-4), 375-402.

Edwards, D., & Rose, V. (1984). Cuticles of *Nematothallus*: a further enigma. *Botanical Journal of the Linnean Society, 88*(1-2), 35-54.

Egerton, P. D. M. G. (1857). Palichthyologic notes. No. 9. On some fish-remains from the neighbourhood of Ludlow. *Quarterly Journal of the Geological Society, 13*(1-2), 282-289.

Eichenberg, W. (1930). Conodonten aus dem Culm des Harzes. *Paläontologische Zeitschrift, 12*(3), 177-182.

Elder, R. L., & Smith, G. R. (1988). Fish taphonomy and environmental inference in paleolimnology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *62*(1-4), 577-592.

Elles, G. L., & Slater, I. L. (1906). The highest Silurian rocks of the Ludlow district. *Quarterly Journal of the Geological Society*, *62*(1-4), 195-222.

Emig, C. C. (1997). Ecology of inarticulated brachiopods. *Treatise on invertebrate paleontology, part H, Brachiopoda (revised)*, *1*, 473-495.

Eriksson, M. E., Nilsson, E. K., & Jeppsson, L. (2009). Vertebrate extinctions and reorganizations during the Late Silurian Lau Event. *Geology*, *37*(8), 739-742.

Esperante, R., Brand, L., Nick, K. E., Poma, O., & Urbina, M. (2008). Exceptional occurrence of fossil baleen in shallow marine sediments of the Neogene Pisco Formation, Southern Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *257*(3), 344-360.

Fang, R. S., Jiang, N. R., Fan, J. C., Cao, R. G., & Li, D. Y. (1985). The middle Silurian and Early Devonian stratigraphy and palaeontology in Qujing District. *Yunnan People's Publishing House, Kunming, Yunnan*.

Fanning, U., Edwards, D., & Richardson, J. B. (1990). Further evidence for diversity in late Silurian land vegetation. *Journal of the Geological Society*, *147*(4), 725-728.

Fanning, U., Edwards, D., & Richardson, J. B. (1991a). A new rhyniophytoid from the late Silurian of the Welsh Borderland. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, *183*, 37-47.

Fanning U, Richardson J.B, Edwards D. (1991b). A review of in situ spores in Silurian land plants. In Pollen and spores, patterns of diversification, Blackmore S., Barnes S.H. (eds). The Systematics Association Special Oxford. Clarendon Press *44*. 25–47.

Ferrón, H. G., & Botella, H. (2017). Squamation and ecology of thelodonts. *PLoS ONE*, *12*(2), e0172781.

Ferrón, H. G., Martínez-Pérez, C., Turner, S., Manzanares, E., & Botella, H. (2018). Patterns of ecological diversification in thelodonts. *Palaeontology*, *61*(2), 303-315.

Finch, W. I., Whitmore, F. C., & Sims, J. D. (1972). *Stratigraphy, morphology, and paleoecology of a fossil peccary herd from western Kentucky*. US Government Printing Office.

Finnegan, S., Bergmann, K., Eiler, J. M., Jones, D. S., Fike, D. A., Eisenman, I., Hughes, N.C., Tripati, A.K & Fischer, W. W. (2011). The magnitude and duration of Late Ordovician–Early Silurian glaciation. *Science*, *331*(6019), 903-906.

Fiorillo, A. R. (1991). Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *81*(3-4), 281-311.

Fiorillo, A. R., McCarthy, P. J., & Flaig, P. P. (2010). Taphonomic and sedimentologic interpretations of the dinosaur-bearing Upper Cretaceous strata of the Prince Creek Formation, northern Alaska: insights from an ancient high-latitude terrestrial ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *295*(3-4), 376-388.

Fisk, H. N., Kolb, C. R., McFarlan, E., & Wilbert, L. J. (1954). Sedimentary framework of the modern Mississippi delta [Louisiana]. *Journal of Sedimentary Research*, *24*(2), 76-99.

Fletcher, T., Altringham, J., Peakall, J., Wignall, P., & Dorrell, R. (2014). Hydrodynamics of fossil fishes. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1788), 20140703.

Flügel, E. (2004). *Microfacies of carbonate rocks: analysis, interpretation and application*. Springer Science & Business Media.

Forey, P. L. (1987). The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Trematáspidae). *Bulletin of the British Museum (Natural History), Geology 41*, 1-30.

Fortey, R. A. (1984). Global earlier Ordovician transgressions and regressions and their biological implications. In *Aspects of the Ordovician System* (Vol. 295, pp. 37-50). Oslo: Universitetsforlaget.

Fretter, V. (1975). *Umbonium vestiarium*, a filter-feeding trochid. *Journal of Zoology*, *177*(4), 541-552.

Fürsich, F. T. (1993). Palaeoecology and evolution of Mesozoic salinity-controlled benthic macroinvertebrate associations. *Lethaia*, *26*(4), 327-346.

Galbany, J., Estebaranz, F., Martínez, L. M., Romero, A., De Juan, J., Turbón, D., & Pérez-Pérez, A. (2006). Comparative analysis of dental enamel polyvinylsiloxane impression and polyurethane casting methods for SEM research. *Microscopy Research and Technique*, *69*(4), 246-252.

Garvey, J. M., & Turner, S. (2006). Vertebrate microremains from the presumed earliest Carboniferous of the Mansfield Basin, Victoria. *Alcheringa*, *30*(1), 43-62.

Gates, T. A. (2005). The Late Jurassic Cleveland-Lloyd dinosaur quarry as a drought-induced assemblage. *Palaios*, *20*(4), 363-375.

Gensel, P. G. (2008). The earliest land plants. *Annual Review of Ecology, Evolution, and Systematics*, *39*, 459-477.

Giffin, E. B. (1979). Silurian vertebrates from Pennsylvania. *Journal of Paleontology*, *53*, 438-445.

Glasspool, I. J., Edwards, D., & Axe, L. (2004). Charcoal in the Silurian as evidence for the earliest wildfire. *Geology*, *32*(5), 381-383.

Gonez, P., & Gerrienne, P. (2010). A new definition and a lectotypification of the genus *Cooksonia* Lang 1937. *International Journal of Plant Sciences*, *171*(2), 199-215.

Gorjansky, W., & Popov, L. (1986). On the origin systematic position of the calcareous-shelled inarticulate brachiopods. *Lethaia*, *19*(3), 233-240.

Goudie, A. (1973). Duricrusts in tropical and subtropical landscapes. Oxford Clarendon Press.

Graham, L.E., Kodner, R.B., Fisher, M.M., Graham, J.M., Wilcox, L.W., Hackney, J.M., Obst, J., Bilkey, P.C., Hanson, D.T. and Cook, M.E., (2004). Early land plant adaptations to terrestrial stress: a focus on phenolics. In *The evolution of plant physiology* (pp. 155-169). Academic Press.

Graham, L. E., Wilcox, L. W., Cook, M. E., & Gensel, P. G. (2004). Resistant tissues of modern marchantioid liverworts resemble enigmatic Early Paleozoic microfossils. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(30), 11025-11029.

Gray, J. E. (1840). Synopsis of the contents of the British Museum. *British Museum, London*. 370pp.

Grellet-Tinner, G. (2005). Membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): implications for exceptional preservation of soft tissue in Lagerstätten. *Journal of Vertebrate Paleontology*, *25*(1), 99-106.

Greig, D. C. (Ed.). (1968). *Geology of the country around Church Stretton, Craven Arms, Wenlock Edge and Brown Clee*. London. HM Stationery Office. 166. pp. 379

Gross, W. (1947). Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica Abteilung A*, *96*, 91-158.

Gross, W. (1957). Mundzähne und hautzähne der acanthodier und arthrodiren. *Palaeontographica Abteilung A*, *109*, 1-40.

Gross, W. (1967). Über Thelodontier-Schuppen. *Palaeontographica Abteilung A*, *127*, 1-67.

Gross, W. (1968). Porenschuppen und Sinneslinien des Thelodontiers *Phlebolepis elegans* Pander. *Paläontologische Zeitschrift*, *42*(3-4), 131-146.

Gross, W. (1971). Downtonische und dittonische Acanthodier-reste des Ostseegebietes. *Palaeontographica Abteilung A*, *136*, 1-82.

Haeckel, E. (1874). *Anthropogenie oder entwickelungsgeschichte des menschen*. Wilhelm Engelmann.

Hagström, J., & Mehlqvist, K. (2012). The dawn of terrestrial ecosystems on Baltica: first report on land plant remains and arthropod coprolites from the upper Silurian of Gotland, Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *317*, 162-170.

Hall, J. (1847). *Palæontology of New-York: Containing descriptions of the organic remains of the lower division of the New-York system* (Vol. 1). C. van Benthuysen. Albany.

Hall, J., Simpson, G. B., & Clarke, J. M. (1859). *Palaeontology of New York* (Vol. 3). C. van Benthuysen. Albany.

Halstead, L. B., & Turner, S. (1973). Silurian and Devonian ostracoderms. *Atlas of palaeobiogeography*, 67-79.

Hansch, W., Siveter, D. J., & Miller, G. (1991). On *Frostiella groenvalliana* Martinsson. *Stereo-Atlas of Ostracod Shells*, *18*, 125-134.

Haq, B. U., & Schutter, S. R. (2008). A chronology of Paleozoic sea-level changes. *Science*, *322*(5898), 64-68.

Harley, J. (1861). On the Ludlow Bone-Bed and its crustacean remains. *Quarterly Journal of the Geological Society*, *17*(1-2), 542-552.

Harper, E. M., Palmer, T. J., & Alphey, J. R. (1997). Evolutionary response by bivalves to changing Phanerozoic sea-water chemistry. *Geological Magazine*, *134*, 403-407.

Hatcher, J. B. (1901). The Jurassic dinosaur deposits near Canyon City, Colorado. *Annals of the Carnegie Museum*, *1*, 327-341.

Hauser, L. M. (2016). An integrated microwave technique for releasing microfossils from an indurated bone bed. *Journal of Micropalaeontology*, *35*(1), 62-65.

Haynes, G. (1988). Mass deaths and serial predation: comparative taphonomic studies of modern large mammal death sites. *Journal of Archaeological Science*, *15*(3), 219-235.

Haynes, G. (1993). *Mammoths, mastodonts, and elephants: biology, behavior and the fossil record*. Cambridge University Press.

Heard, A. (1939). Further notes on Lower Devonian plants from south Wales. *Quarterly Journal of the Geological Society*, *95*(1-4), 223-229.

Henningsmoen, G. (1953). Classification of Paleozoic straight-hinged ostracods. *Norsk Geologisk Tidsskrift*, *31*, 185-288.

Hoffman, R. (1988). The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology*, *14*(1), 81-90.

Holland, H.C. & Bassett, M. G. (1989). *A global standard for the Silurian System*. National Museum of Wales.

Holland, H.C., Lawson, J.D. & Walmsley,V.G. (1963).The Silurian Rocks of the Ludlow District. *Bulletin of the British Museum (Natural History): Geology*, *8*, 93–171.

Hook, R. W., & Ferm, J. C. (1988). Paleoenvironmental controls on vertebrate-bearing abandoned channels in the Upper Carboniferous. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *63*(1-3), 159-181.

Hoppe, K. H. (1931). Die Coelolepiden und Acanthodier des Obersilurs der Insel Ösel. Ihre Paläobiologie und Paläontologie. *Palaeontographica*, *76*, 35-94.

Howell, J. V. (1957). Glossary of geology and related sciences: Washington, DC. *American Geological Institute, NASNRC Publication*.

Hueber, F. M. (2001). Rotted wood–alga–fungus: the history and life of *Prototaxites* Dawson 1859. *Review of Palaeobotany and Palynology*, *116*(1), 123-158.

Hunt, A. P. (1986). Taphonomy of the Cleveland Lloyd Quarry, Morrison Formation (late Jurassic), Emery County, Utah: a preliminary report. In *Abstracts with Programs, Fourth North American Paleontological Convention, Boulder, Colorado A* (Vol. 21).

Huttenlocker, A. K., Henrici, A., Nelson, W. J., Elrick, S., Berman, D. S., Schlotterbeck, T., & Sumida, S. S. (2018). A multitaxic bonebed near the Carboniferous–Permian boundary (Halgaito Formation, Cutler Group) in Valley of the Gods, Utah, USA: Vertebrate paleontology and taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *499*, 72-92.

Huxley, T. H. (1858). On *Cephalaspis* and *Pteraspis*. *Quarterly Journal of the Geological Society*, *14*(1-2), 267-280.

Ingham, J. K., Cope, J. C. W., & Rawson, P. F. (Eds.). (1999). *Atlas of palaeogeography and lithofacies*. Geological Society of London.

Jaekel, O. M. J. (1911). *Die wirbeltiere; eine übersicht über die fossilen und lebenden formen*. Gebrüder Borntraeger, Berlin, 252.

Janvier, P., Halstead, L. B., & Westoll, T. S. (1985). Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *309*(1138), 259-272.

Janvier, P., & Melo, J. H. G. (1988). Acanthodian fish remains from the Upper Silurian or Lower Devonian of the Amazon basin, Brazil. *Palaeontology*, *31*(3), 771-777.

Jarochowska, E., Munnecke, A., & Kozłowski, W. (2014). An unusual microbial-rostroconch assemblage from the Mulde Event (Homerian, middle Silurian) in Podolia, Western Ukraine. *GFF*, *136*(1), 120-124.

Jeppsson, L. & Laufeld, S. (1986) The late Silurian Öved-Ramsåsa Group in Skåne, South Sweden. *Sveriges Geologiska Undersökning, 58*, 1–45.

Jeppsson, L., Talent, J.A., Mawson, R., Andrew, A., Corradini, C., Simpson, A.J., Wigforss-Lange, J. and Schönlaub, H.P., (2012). Late Ludfordian correlations and the Lau event. In *Earth and life* (pp. 653-675). Springer, Dordrecht.

Jeram, A. J., Selden, P. A., & Edwards, D. (1990). Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, *250*(4981), 658-661.

Jones, T. R. (1855). XIV.—Notes on Palaeozoic bivalved Entomostraca. No. II. Some British and foreign species of *Beyrichia*. *Journal of Natural History*, *16*(93), 163-176.

Jones, T. R. (1856). Notes on the Palaeozoic bivalved Entomostraca No. 3, some species of *Leperditia*. *Annals and Magazine of Natural History, Series 2, 17*, 81-101.

Jonker, F. P. (1979). Prototaxites in the lower Devonian. *Palaeontographica Abteilung B, 171* 551-562.

Kaljo, D., Einasto, R., Martma, T., Märss, T., Nestor, V., & Viira, V. (2015). A bio-chemostratigraphical test of the synchroneity of biozones in the upper Silurian of Estonia and Latvia with some implications for practical stratigraphy. *Estonian Journal of Earth Sciences*, *64*(4), 267.

Karatajūtė-Talimaa, V. N. (1978). *Silurian and Devonian thelodonts of the USSR and Spitsbergen*. Mokslas, Vilnius.

Karatajutė-Talimaa, V. (1997). Taxonomy of loganiid thelodonts. *Modern Geology*, *21*(1), 1-16.

Karatajūtė-Talimaa, V., & Märss, T. (2002). Upper Silurian thelodonts from Severnaya Zemlya Archipelago (Russia). *Geodiversitas*, *24*(2), 405-443.

Keating, J. N., Marquart, C. L., & Donoghue, P. C. (2015). Histology of the heterostracan dermal skeleton: insight into the origin of the vertebrate mineralised skeleton. *Journal of Morphology*, *276*(6), 657-680.

Keating, J. N., Sansom, R. S., & Purnell, M. A. (2012). A new osteostracan fauna from the Devonian of the Welsh Borderlands and observations on the taxonomy and growth of Osteostraci. *Journal of Vertebrate Paleontology*, *32*(5), 1002-1017.

Kenrick, P., & Crane, P. R. (1997). The origin and early evolution of plants on land. *Nature*, *389*(6646), 33-39.

Kiaer, J. (1931). *Hemicyclaspis murchisoni*-Faunaen i den Downtoniske Sandsten på Jeløen i Oslo Fjorden. *Norsk Geologisk Tidsskrift*, *12*, 419-433.

Kiaer, J., (1932) New coelolepids from the Upper Silurian on Oesel (Esthonia). *Eesti Loodusteaduse Arhiiv, Seeria 1*(10), 167-176.

Kidwell, S. M. (1986). Models for fossil concentrations: paleobiologic implications. *Paleobiology*, *12*(1), 6-24.

Kidwell, S. M. (1989). Stratigraphic condensation of marine transgressive records: origin of major shell deposits in the Miocene of Maryland. *The Journal of Geology*, *97*(1), 1-24.

Kidwell, S.M. (1991a). The stratigraphy of shell concentrations. Pp. 211–290 In *Taphonomy: Releasing the data locked in the fossil record*. *Topics in Geobiology* 9. P.A. Allison and D.E.G. Briggs, (eds.) Plenum Publishing, New York.

Kidwell, S.M. (1991b). Condensed deposits in siliciclastic sequences: Expected and observed features. Pp. 682–695 *In Cycles and events in stratigraphy*. G. Einsele, W. Ricken, and A. Seilacher, (eds.) *Springer Verlag*, Berlin.

Kidwell, S. M. (1993). Taphonomic expressions of sedimentary hiatuses: field observations on bioclastic concentrations and sequence anatomy in low, moderate and high subsidence settings. *Geologische Rundschau*, *82*(2), 189-202.

Kidwell, S. M. (2005). Brachiopod versus bivalve radiocarbon ages: implications for Phanerozoic trends in time-averaging and productivity. In *Geological Society of America Abstracts 37*(7), 117.

Kidwell, S. M., & Behrensmeyer, A. K. (1988). Overview: ecological and evolutionary implications of taphonomic processes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *63*(1-3), 1-13.

Kidwell, S. M., Bosence, D. W., Allison, P. A., & Briggs, D. E. G. (1991). Taphonomy and time-averaging of marine shelly faunas. *Taphonomy: releasing the data locked in the fossil record.* Plenum, New York, 115-209.

Kidwell, S. M., Fürsich, R. T., & Algner, T. (1986). Conceptual framework for the analysis and classification of fossil concentrations. *Palaios*, 1, 228-238.

King, W. (1846). XI.—Remarks on certain genera belonging to the class Palliobranchiata. *Journal of Natural History*, *18*(117), 83-94.

King, W.W. (1934). The Downtonian and Dittonian strata of Great Britain and north-western Europe. *Quarterly Journal of the Geological Society*, *90*(1-4), 526-566.

Kjellesvig-Waering, E. N. (1961). The Silurian Eurypterida of the Welsh Borderland. *Journal of Paleontology*, *34*(4) 789-835.

Knaust, D. (2017). *Atlas of trace fossils in well core: appearance, taxonomy and interpretation*. Springer.

Knaust, D. (2018). The ichnogenus *Teichichnus* Seilacher, 1955. *Earth-Science Reviews, 177*, 386-403.

Kodner, R. B., & Graham, L. E. (2001). High-temperature, acid-hydrolyzed remains of Polytrichum (Musci, Polytrichaceae) resemble enigmatic Silurian-Devonian tubular microfossils. *American Journal of Botany*, *88*(3), 462-466.

Koninick, L. (1881). Faune du calcaire carbonifère de Belgique, Pt. 3, Gastéropodes. In *Annales du Musée royal d'Histoire naturelle de Belgique, Paleontological Series* (Vol. 6, pp. 1-170).

Korth, W. W. (1979). Taphonomy of microvertebrate fossil assemblages. *Annals of the Carnegie Museum*, *48*, 235–285.

Koster, E. H. (1987). Vertebrate taphonomy applied to the analysis of ancient fluvial systems. Pp. 159–168. *In Recent developments in fluvial sedimentology*. Special publication 39. F.G. Ethridge, R.M. Flores, and M.D. Harvey, (eds.) Society of Economic Paleontologists and Mineralogists.

Kräusel, R. (1936). Landbewohnende Algenbäume zur Devonzeit? *Berichte der Deutschen Botanischen* Gesellschaft, 54, 379–385.

Kříž, J. (1984). Autecology and ecogeny of Silurian Bivalvia. *Special Papers in Palaeontology*, *32*, 71-85.

Kusmer, K. D. (1990). Taphonomy of owl pellet deposition. *Journal of Paleontology*, *64*(4), 629-637.

Lamarck, J. B. D. M. (1801). *Systeme des animaux sans vertèbres: ou tableau général des classes, des ordres et des genres de ces animaux...: précédé du discours d'ouverture du cours de zoologie...* Determille. Paris, 432 pp., pls, 1-6.

Lang, W. H. (1937). On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *227*(544), 245-291.

Lang, W. H. (1945). The Hooker Lecture.—*Pachytheca* and some anomalous early plants (*Prototaxites*, *Nematothallus*, *Parka*, *Foerstia*, *Orvillea* ng). *Botanical Journal of the Linnean Society*, *52*(347), 535-552.

Lankester, E. R. (1873). I.—On *Holaspis sericeus*, and on the relationships of the fish-genera *Pteraspis*, *Cyathaspis*, and *Scaphaspis*. *Geological Magazine*, *10*(108), 241-245.

Lankester, E. R., & Traquair, R. H. (1914). A monograph the fishes of the Old Red Sandstone of Britain. Part I.—The Cephalaspidæ. Part II.—The Asterolepidæ. *Monographs of the Palaeontographical Society*, *67*(332), 131-134.

Lapworth, C. (1879). I.—On the tripartite classification of the Lower Palaeozoic rocks. *Geological Magazine*, *6*(1), 1-15.

Latreille, P. A. (1802). *Histoire naturelle des Crustacés et des insectes. 3 Familles naturelles des genres*. Dufart, Paris. pp. 468.

Laudet, F., & Selva, N. (2005). Ravens as small mammal bone accumulators: First taphonomic study on mammal remains in raven pellets. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *226*(3-4), 272-286.

Lawson, J.D. & White, D.E. (1989). Standard Ludlow Series. In Holland, C.H, Bassett, & M.G. (eds). *A global standard for the Silurian System. National Museum of Wales, Cardiff. Geological Series*, *9*, 73-90.

Lawton, R. (1977). Taphonomy of the dinosaur quarry, Dinosaur National Monument. *Rocky Mountain Geology*, *15*(2), 119-126.

Leggitt, V. L., & Buchheim, H. P. (1997). Bird bone taphonomic data from recent lake margin strandlines compared with an Eocene Presbyornis (Aves: Anseriformes) bone strandline. In *Geological Society of America Abstracts with Programs*. *29*(6), A105.

Lehman, J. P. (1937). Les poissons du Downtonien de la Scanie (Suède)*: Mémoire Facultie Science Universitie Paris*, 1-98.

Le Rock, J. W. (2000). Sedimentology and taphonomy of a dinosaur bonebed from the Upper Cretaceous (Campanian) Judith River Formation of north central Montana (Doctoral dissertation, Montana State University-Bozeman, College of Letters & Science).

Lindström, G. (1884). On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Veternskaps-Akademiens Handlinger*. Bandet, 19(6), pp.250.

Ling, M. X., Zhan, R. B., Wang, G. X., Wang, Y., Amelin, Y., Tang, P., Liu, J.B., Jin, J., Huang, B, Wu, R.C., Xue, S., Fu, B., Bennett, V.C., Wei, X., Luan, X.C., Finnegan, S., Harper, D. A.T. & Rong, J.Y. (2019). An extremely brief end Ordovician mass extinction linked to abrupt onset of glaciation. *Solid Earth Sciences*, *4*(4), 190-198.

Linnaeus, C. V. (1758). *Systema naturae*, 10th edn, vol. 1. Stockholm: L. Salvii.

Llewellyn, R. (2015). *Palynology through the early Wenlock Ireviken Event* (Doctoral dissertation, University of Portsmouth).

Loeffler, E. J., & Dineley, D. L. (1976). A new species of *Corvaspis* (Agnatha, Heterostraci) from the upper Silurian to lower or middle Devonian of the North-west Territories, Canada. *Palaeontology*, *19*(4), 757-766.

Long, J. A. (1986). A new Late Devonian acanthodian fish from Mt. Howitt, Victoria, Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society of Victoria*, *98*(1-2), 1-17.

Long, J. A. (2011). The *rise of fishes*. (2nd ed). Baltimore. John Hopkins University Press.

Lorenz, H., Gee, D. G., & Simonetti, A. (2008). Detrital zircon ages and provenance of the Late Neoproterozoic and Palaeozoic successions on Severnaya Zemlya, Kara Shelf: a tie to Baltica. *Norwegian Journal of Geology*, *88*(4), 235-258.

Loydell, D. K. (1998). Early Silurian sea-level changes. *Geological Magazine*, *135*(4), 447-471.

Loydell, D. K. (2007). Early Silurian positive $\delta^{13}C$ excursions and their relationship to glaciations, sea-level changes and extinction events. *Geological Journal*, *42*(5), 531-546.

Loydell, D. K., & Frýda, J. (2011). At what stratigraphical level is the mid Ludfordian (Ludlow, Silurian) positive carbon isotope excursion in the type Ludlow area, Shropshire, England? *Bulletin of Geosciences*, *86*(2), 197-208.

Lyman, R. L., & Lyman, C. (1994). *Vertebrate taphonomy*. Cambridge University Press.

MacEachern, J. A., & Gingras, M. K. (2006). Recognition of brackish-water trace-fossil suites in the Cretaceous Western Interior Seaway of Alberta, Canada. *Special Publication-SEPM*, *88*, 149-194.

Macquaker, J. H. S. (1994). Palaeoenvironmental significance of 'bone-beds' in organic-rich mudstone successions: an example from the Upper Triassic of south-west Britain. *Zoological Journal of the Linnean Society*, *112*(1-2), 285-308.

Maidment, S. C., Kirkpatrick, C., Craik-Smith, B., & Blythe, J. E. (2017). A new ornithischian dinosaur and the terrestrial vertebrate fauna from a bone bed in the Wealden of Ardingly, West Sussex. *Proceedings of the Geologists' Association*, *128*(3), 332-339.

Mallon, J. C., Henderson, D. M., McDonough, C. M., & Loughry, W. J. (2018). A "bloat-and-float" taphonomic model best explains the upside-down preservation of ankylosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *497*, 117-127.

Manda, Š. Štorch, P., Slavik, L., Frýda, J., Kříž, J., & Tasaryova, Z. (2012). The graptolite, conodont and sedimentary record through the late Ludlow Kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia. *Geological Magazine*, *149*(3), 507-531.

Manning, P. L. (1993). *Palaeoecology of the eurypterids of the Upper Silurian of the Welsh Borderlands* (Doctoral dissertation, University of Manchester).

Manning, P. L., & Dunlop, J. A. (1995). The respiratory organs of eurypterids. *Palaeontology*, *38*(2), 287-298.

Märss, T. (1986). Squamation of the thelodont agnathan *Phlebolepis*. *Journal of Vertebrate Paleontology*, *6*(1), 1-11.

Märss, T. (1990). Vertebrates. In *Field Meeting, Estonia. An Excursion Guidebook*, pp. 93-96. Institute of Geology, Estonian Academy of Sciences, Tallinn. pp. 209.

Märss, T. (1992). Vertebrate history in the Late Silurian. *Proceedings of the Estonian Academy of Sciences, Geology 41*(4), pp. 205-214.

Märss, T. (2001). *Andreolepis* (Actinopterygii) in the upper Silurian of northern Eurasia. In *Proceedings of the Estonian Academy of Sciences, Geology*, *50*(3), 174-189.

Märss, T. (2011). A unique Late Silurian *Thelodus* squamation from Saaremaa (Estonia) and its ontogenetic development. *Estonian Journal of Earth Sciences*, *60*(3), 137-146.

Märss, T., Caldwell, M., Gagnier, P. Y., Goujet, D., Männik, P., Martma, T., & Wilson, M. (1998). Distribution of Silurian and Lower Devonian vertebrate microremains and conodonts in the Baillie-Hamilton and Cornwallis Island sections, Canadian Arctic. *Proceedings of the Estonian Academy of Sciences, Geology* (Vol. *47*(2), 51-76.

Märss, T., & Einasto, R. (1978). Distribution of vertebrates in deposits of various facies in the North Baltic Silurian. *Izvestiâ Aka− demii Nauk Estonskoj SSR. Geologiâ*, *27*, 16-22.

Märss, T., Fredholm, D., Talimaa, V., Turner, S., Jeppsson, L., & Nowlan, G. (1995). Silurian vertebrate biozonal scheme. *Geobios*, *28*, 369-372.

Märss, T., Karatajūtė-Talimaa, V., & Turner, S. (2007). *Handbook of paleoichthyology: Agnatha-2. Thelodonti*. Fischer. Edited by H-P. Schultze. Gustav Fischer Verlag, Stuttgart. New York, 143 pp.

Märss, T., & Männik, P. (2013). Revision of Silurian vertebrate biozones and their correlation with the conodont succession. *Estonian Journal of Earth Sciences*, *62*(4), 181-204.

Märss, T., & Miller, C. G. (2004). Thelodonts and distribution of associated conodonts from the Llandovery–lowermost Lochkovian of the Welsh Borderland. *Palaeontology*, *47*(5), 1211-1265.

Märss, T., Perens, H., & Klaos, T. (2003). Sedimentation of the Himmiste-Kuigu fish bed (Ludlow of Estonia), and taphonomy of the *Phlebolepis elegans* Pander (Thelodonti) shoal. *Proceedings of the Estonian Academy of Sciences, Geology* 52(4), 239-265.

Märss, T., & Ritchie, A. (1998). Articulated thelodonts (Agnatha) of Scotland. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *88*(3), 143-195.

Märss, T., Wilson, M. V., & Thorsteinsson, R. (2002). New thelodont (Agnatha) and possible chondrichthyan (Gnathostomata) taxa established in the Silurian and Lower Devonian of the Canadian Arctic Archipelago. *Proceedings of the Estonian Academy of Sciences, Geology*, *51*(2), 88-120.

Marston, A. (1882) *Guide to the geology of Ludlow*. Privately Published, Ludlow.

Martill, D. M. (1985). The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences*, *311*(1148), 155-165.

Martill, D. M. (1991). Bones as stones: the contribution of vertebrate remains to the lithologic record. *The processes of fossilization*, 270-292.

Martill, D. M., Batten, D. J., & Loydell, D. K. (2000). A new specimen of the thyreophoran dinosaur cf. *Scelidosaurus* with soft tissue preservation. *Palaeontology*, *43*(3), 549-559.

Martill, D. M., Naish, D., & Earland, S. (2006). Dinosaurs in marine strata: evidence from the British Jurassic, including a review of the allochthonous vertebrate assemblage from the marine Kimmeridge Clay Formation (Upper Jurassic) of Great Britain. *Actas de las III Jornadas sobre Dinosaurios y su Entorno. Salas de los Infantes, Burgos*, *47*, 83.

Martinsson, A. (1962). The concealed Silurian of the Baltic area. *Geologiska Föreningen i Stockholm Förhandlingar*, *84*(4), 539-545.

Martinsson, A. (1963). *Kloedenia* and related ostracode genera in the Silurian and Devonian of the Baltic area and Britain. *Bulletin of the Geological Institutions of the University of Uppsala*. *42*, 1-63.

Massa, D., Havlíček, V., & Bonnefous, J. (1977). Stratigraphic and faunal data on the Ordovician of the Rhadames Basin (Libya and Tunisia). *Bulletin des Centres de Recherches Exploration−Production Elf−Aquitaine*, *1*, 3-27.

Mathews, J. C., Brusatte, S. L., Williams, S. A., & Henderson, M. D. (2009). The first *Triceratops* bonebed and its implications for gregarious behavior. *Journal of Vertebrate Paleontology*, *29*(1), 286-290.

Matthew, G. F. (1886). Illustrations of the fauna of the St. John Group continued: No. 3: On the Conocoryphaea, with further remarks on *Paradoxides*. *Transactions of the Royal Society of Canada*, *1*(3,4), 29-84.

Matthew, W. D. (1923). Fossil bones in the rock. *Natural History*, *23*(4), 358-369.

Mattson Jr, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, *11*(1), 119-161.

Mayhew, D. F. (1977). Avian predators as accumulators of fossil mammal material. *Boreas*, *6*(1), 25-31.

McConnell, B., Riggs, N., & Sevastopulo, G. (2019). Insight into late Iapetus tectonics from new U–Pb zircon and micropalaeontological data from the Navan area, eastern Ireland. *Journal of the Geological Society*, *176*(3), 440-446.

McCoy, F. (1853). On the supposed fish remains figured on Plate 4 of the 'Silurian System'. *Quarterly Journal of the Geological Society*, *9*(1-2), 12-15.

McKerrow, W. S., Mac Niocaill, C., & Dewey, J. F. (2000). The Caledonian orogeny redefined. *Journal of the Geological Society*, *157*(6), 1149-1154.

Melchin, M. J., & Macrae, R. A. (2005). The stratigraphy and paleontology of the Ordovician–Silurian Arisaig Group. In *Nova Scotia: Field Trip Guide, North American Paleontology Convention: Halifax, NS*.

Mihlbachler, M. C., Campbell, D., Chen, C., Ayoub, M., & Kaur, P. (2018). Microwear–mesowear congruence and mortality bias in rhinoceros mass-death assemblages. *Paleobiology*, *44*(1), 131-154.

Miles, R. S. (1973). Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum (Natural History) Geology Series*, *24*, 133-213.

Miller, C. G. (1995a). Ostracode and conodont distribution across the Ludlow/Přídolí boundary of Wales and the Welsh Borderland. *Palaeontology*, *38*(2), 341-384.

Miller, C. G. (1995b). Data associated with the paper 'ostracods and content distribution across the Ludlow/Přídolí boundary of Wales and the Welsh Borderlands in *Palaeontology*. *Supplementary Publication of the British Library*, *38*, 341-384.

Miller, C. G., & Märss, T. (1999). A conodont, thelodont and acanthodian fauna from the Lower Přídolí (Silurian) of the Much Wenlock Area, Shropshire. *Palaeontology*, *42*(4), 691-714.

Miller, C. G., Sutherland, S. J., & Dorning, K. J. (1997). Late Silurian (Ludlow–Přidoli) microfossils and sedimentation in the Welsh Basin near Clun, Shropshire. *Geological Journal*, *32*(1), 69-83.

Miller, S. A. (1877). *The American Palaeozoic fossils: a catalogue of the genera and species, with names of authors, dates, places of publication, groups of rocks in which found, and the etymology and signification of the words, and an introduction devoted to the stratigraphical geology of the Palaeozoic rocks*. Published by the author, Cincinnati, Ohio, 15. 245 pp.

Moberg, J. C., & Grönwall, K. A. (1909). Om Fyledalens Gotlandium: Lunds Universitets Årsskrift., *NF*, *2*, 1–86.

Morlan, R. E. (1984). Toward the definition of criteria for the recognition of artificial bone alterations 1. *Quaternary Research*, *22*(2), 160-171.

Morris, J. L., Richardson, J. B., & Edwards, D. (2011). Lower Devonian plant and spore assemblages from Lower Old Red Sandstone strata of Tredomen Quarry, South Wales. *Review of Palaeobotany and Palynology*, *165*(3), 183-208.

Morrissey, L. B., Braddy, S. J., Bennett, J. P., Marriott, S. B., & Tarrant, P. R. (2004). Fish trails from the lower Old Red Sandstone of Tredomen Quarry, Powys, southeast Wales. *Geological Journal*, *39*(3-4), 337-358.

Mukherjee, D., & Ray, S. (2012). Taphonomy of an Upper Triassic vertebrate bonebed: a new rhynchosaur (Reptilia; Archosauromorpha) accumulation from India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *333*, 75-91.

Muller, J. (1959). Palynology of recent Orinoco delta and shelf sediments: reports of the Orinoco shelf expedition; *Micropaleontology*, *5*, 1-32.

Munnecke, A., Calner, M., Harper, D. A., & Servais, T. (2010). Ordovician and Silurian sea–water chemistry, sea level, and climate: a synopsis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *296*(3-4), 389-413.

Murchison, R. I. (1839). *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford: with descriptions of the coalfields and overlying formations* (Vol. 1). J. Murray. London, 768 pp.

Murchison, R. I. (1853). On some of the remains in the Bone-bed of the Upper Ludlow Rock. *Quarterly Journal of the Geological Society*, *9*(1-2), 16-17.

Murchison, R. I. (1859). *Siluria: the history of the oldest fossiliferous rocks and their foundations; with a brief sketch of the distribution of gold over the Earth*. Murray. London, 731 pp.

Murchison, R. I. (1867). *Siluria: a history of the oldest rocks in the British Isles and other countries; with sketches of the origin and distribution of native gold, the general succession of geological formations, and changes of the Earth's surface*. J. Murray, London, 566 pp.

Newell, N.D. (1969). Subclass Anomalodesmata. In: R.C. Moore and C. Teichert (eds.), *Treatise on Invertebrate Paleontology.* The Geological Society of America, Inc., and The University of Kansas, *Part N, 2, Mollusca* 6, Bivalvia, p. 818.

Newman, M. J., Burrow, C. J., Davidson, R. G., den Blaauwen, J. L., & Jones, R. (2017). Comparison of the vertebrate faunas of the Lower Old Red Sandstone of the Anglo-Welsh Basin with contemporary faunas in Scotland. *Proceedings of the Geologists' Association*, *128*(3), 447-459.

Nicholson, H. A. (1872). Contributions to the study of the errant Annelides of the older Palaeozoic rocks. *Proceedings of the Royal Society of London*, *21*(139-147), 288-290.

Niklas, K. J., & Smocovitis, V. (1983). Evidence for a conducting strand in early Silurian (Llandoverian) plants: implications for the evolution of the land plants. *Paleobiology*, *9*(2), 126-137.

Norell, M. A., Clark, J. M., Chiappe, L. M., & Dashzeveg, D. (1995). A nesting dinosaur. *Nature*, *378*(6559), 774.

Norman, D. B. (2000). Professor Richard Owen and the important but neglected dinosaur *Scelidosaurus harrisonii*. *Historical Biology*, *14*(4), 235-253.

Nützel, A., Joachimski, M., & Correa, M. L. (2010). Seasonal climatic fluctuations in the Late Triassic tropics—High-resolution oxygen isotope records from aragonitic bivalve shells (Cassian Formation, Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *285*(3-4), 194-204.

Ogg, J. G., Ogg, G., & Gradstein, F. M. (2016). *A concise geologic time scale: 2016*. Elsevier.

Okulitch, A. V., Packard, J. J., & Zolnai, A. I. (1986). Evolution of the Boothia Uplift, Arctic Canada. *Canadian Journal of Earth Sciences*, *23*(3), 350-358.

Owen, R. (1846). *Lectures on the comparative anatomy and physiology of the vertebrate Animals*: Delivered at the Royal College of Surgeons of England, in 1844 and 1846 (Vol. 2). Longman, Brown, Green, and Longmans. London.

Page, D. (1859). *Handbook of geological terms and geology*. W. Blackwood and sons.

Pander, C. H. (1856). *Monographie der fossilen Fische des silurischen Systems des Russisch-baltischen Gouvernements* (Vol. 1). Buchdr. der K. Akademie der Wissenschaften.

Parsons, K. M., Brett, C. E., & Miller, K. B. (1988). Taphonomy and depositional dynamics of Devonian shell-rich mudstones. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *63*(1-3), 109-139.

Peel, J. S. (1984). Autecology of Silurian gastropods and monoplacophorans. *Special Papers in Palaeontology*, *32*, 71-85.

Perales-Gogenola, L., Elorza, J., Canudo, J. I., & Pereda-Suberbiola, X. (2019). Taphonomy and palaeohistology of ornithischian dinosaur remains from the Lower Cretaceous bonebed of La Cantalera (Teruel, Spain). *Cretaceous Research*, *98*, 316-334.

Perrier, V., & Siveter, D. J. (2013). Testing Silurian palaeogeography using 'European'ostracod faunas. *Geological Society, London, Memoirs*, *38*(1), 355-364.

Peterson, O.A. (1906). The Agate Spring fossil quarry. *Annals of the Carnegie Museum*, *3*(4), 487-494.

Phillips, J., & Salter, J. W. (1848). Palaeontological appendix to Professor John Phillips' Memoir on the Malvern Hills compared with the Palaeozoic districts of Abberley etc. *Memoir of the Geological Survey of Great Britain*, *2*(1), 331-386.

Pokorný, (1954). *Zdklady zoologicke mikropaleontologie*. Ceskoslovenske Akadamiya, Prague.

Potts, R., Behrensmeyer, A. K., & Ditchfield, P. (1999). Paleolandscape variation and Early Pleistocene hominid activities: members 1 and 7, Olorgesailie Formation, Kenya. *Journal of Human Evolution*, *37*(5), 747-788.

Powrie, J. (1870). On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone rocks of Forfarshire. *Transactions of the Edinburgh Geological Society*, *1*(3), 284-301.

Prothero, D. R., & Schwab, F. (2004). *Sedimentary geology*. Macmillan.

Racheboeuf, P. R., Vannier, J., Schram, F. R., Chabard, D., & Sotty, D. (2008). The euthycarcinoid arthropods from Montceau-les-Mines, France: functional morphology and affinities. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, *99*(1), 11-25.

Reading, H. G. (Ed.). (2009). *Sedimentary environments: processes, facies and stratigraphy*. John Wiley & Sons.

Reed, F. O. (1934). Downtonian fossils from the Anglo-Welsh area. *Quarterly Journal of the Geological Society*, *90*(1-4), 571-584.

Reif, W. E. (1969). *Bonebeds an der Muschelkalk-Keuper-Grenze in Ostwürttemberg.-Dipl* (Doctoral dissertation, Thesis (unpubl.) 123 pp., University of Tübingen).

Reif, W. E. (1976). Sedimentologie und Genese von Bonebeds. *Zentralblatt für Geologie und Paläontologie*, *5*, 252-255.

Reif, W. E. (1982). Muschelkalk/Keuper bone-beds (Middle Triassic, SW-Germany)—storm condensation in a regressive cycle. In *Cyclic and event stratification.* Springer, Berlin, Heidelberg. 299-325

Reynolds, S. H. (1928). Breccias. *Geological Magazine*, *65*(3), 97-107.

Richardson, J. B., & Lister, T. R. (1969). Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and south Wales. *Palaeontology*, *12*(2), 201-245.

Richardson, J. B., & Rasul, S. M. (1990). Palynofacies in a Late Silurian regressive sequence in the Welsh Borderland and Wales. *Journal of the Geological Society*, *147*(4), 675-686.

Ritchie, A. (1968). *Phlebolepis elegans* Pander, an Upper Silurian thelodont from Oesel, with remarks on the morphology of thelodonts. In *Current problems of lower vertebrate phylogeny: proceedings of the Fourth Nobel Symposium*. Almqvist & Wiskell. 4, 81-8.

Roberts, G. (1842). *An etymological and explanatory dictionary of the terms and language of geology: designed for the early student, and those who have not made progress in the science.* Longman, Orme, Brown, Green, & Longmans.

Roberts, G. E. (1861). On the distribution of *Cephalaspis* and *Pteraspis* in England. *The Geologist*, *4*(3), 102-109.

Roberts, G. E., & Randall, J. (1863). On the Upper Silurian Passage-beds at Linley, Salop. *Quarterly Journal of the Geological Society*, *19*(1-2), 229-232.

Rodríguez-Cabello, C., Sánchez, F., & Olaso, I. (2007). Distribution patterns and sexual segregations of *Scyliorhinus canicula* (L.) in the Cantabrian Sea. *Journal of Fish Biology*, *70*(5), 1568-1586.

Rogers, R. R. (1990). Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality. *Palaios*, 394-413.

Rogers, R. R. (1995). *Sequence stratigraphy and vertebrate taphonomy of the Upper Cretaceous Two Medicine and Judith River formations, Montana* (Doctoral dissertation, University of Chicago, Department of the Geophysical Sciences).

Rogers, R. R., Arcucci, A. B., Abdala, F., Sereno, P. C., Forster, C. A., & May, C. L. (2001). Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), northwestern Argentina: spectacular preservation in volcanogenic concretions. *Palaios*, *16*(5), 461-481.

Rogers, R. R. & Brady, M. E. (2010). Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north-central Montana. *Paleobiology*, *36*(1), 80-112.

Rogers, R. R., Eberth, D. A., & Fiorillo, A. R. (Eds.). (2007). *Bonebeds: genesis, analysis, and paleobiological significance*. University of Chicago Press.

Rogers, R. R., & Kidwell, S. M. (2000). Associations of vertebrate skeletal concentrations and discontinuity surfaces in terrestrial and shallow marine records: a test in the Cretaceous of Montana. *The Journal of Geology*, *108*(2), 131-154.

Rogers, R. R., & Kidwell, S. M. (2007). A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations. *Bonebeds: Genesis, analysis, and paleobiological significance*, 1-63.

Rogers, R. R., Krause, D. W., Kast, S. C., Marshall, M. S., Rahantarisoa, L., Robins, C. R., & Sertich, J. J. (2013). A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. *Cretaceous Research*, *44*, 12-29.

Rogerson, E. C. W., Edwards, D., Axe, L., & Davies, K. L. (2002). A new embryophyte from the Upper Silurian of Shropshire, England. *Special Papers in Palaeontology*, *67*, 233-249.

Rogerson, E. C. W., Edwards, D., Davies, K. L., & Richardson, J. B. (1993). Identification of in situ spores in a Silurian *Cooksonia* from the Welsh Borderland. *Special Papers in Palaeontology*, *49*, 17-30.

Rose, J. J. (1983). A replication technique for scanning electron microscopy: applications for anthropologists. *American Journal of Physical Anthropology*, *62*(3), 255-261.

Rouault, M. (1851). *Mémoire sur le terrain paléozoïque des environs de Rennes*. L. Martinet.

Runnegar, B. (1985). Shell microstructures of Cambrian molluscs replicated by phosphate. *Alcheringa*, *9*(4), 245-257.

Ryan, M. J., Russell, A. P., Eberth, D. A., & Currie, P. J. (2001). The taphonomy of a *Centrosaurus* (Ornithischia: Certopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. *Palaios*, *16*(5), 482-506.

Saarnisto, M., & Ojala, A. E. (2009). Varved sediments. *Encyclopedia of Paleoclimatology and Ancient Environments*, 973-975.

Sahni, A. (1972). The vertebrate fauna of the Judith River Formation, Montana. *Bulletin of the American museum natural history*; *147*(6), p. 325.

Sallan, L., Friedman, M., Sansom, R. S., Bird, C. M., & Sansom, I. J. (2018). The nearshore cradle of early vertebrate diversification. *Science*, *362*(6413), 460-464.

Salter, J. W. (1852). Description of the *Pterygotus problematicus*, Agass. *Quarterly Journal of the Geological Society*, *8*(1-2), 386-388.

Sander, P. M. (1987). Taphonomy of the Lower Permian Geraldine bonebed in Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *61*, 221-236.

Sansom, I. J., Smith, M. P., Smith, M. M., & Turner, P. (1995). The Harding Sandstone revisited-a new look at some old bones. *Geobios*, *28*, 57-59.

Sansom, R. (2007). A review of the problematic osteostracan genus *Auchenaspis* and its role in thyestidian evolution. *Palaeontology*, *50*(4), 1001-1011.

Schaarschmidt, F. (1974). *Mosellophyton hefteri* ngn sp.(? Psilophyta), ein sukkulenter Halophyt aus dem Unterdevon von Alken an der Mosel. *Paläontologische Zeitschrift*, *48*(3), 188-204.

Schäfer, W. (1962). *Aktuo-paläontologie nach Studien in der Nordsee* (No. 41). W. Kramer.

Schäfer, W. (1972). *Ecology and palaeoecology of marine environments*, translated by I. Oertel, edited by GY Craig: University of Chicago Press, Chicago.

Schimmelmann, A., Lange, C. B., Schieber, J., Francus, P., Ojala, A. E., & Zolitschka, B. (2016). Varves in marine sediments: a review. *Earth-Science Reviews*, *159*, 215-246.

Schmidt, W. (1958). Pflanzenreste aus der Tonschiefer-Gruppe (Unteres Siegen) des Siegerlandes. II. *Pachytheca reticulata* Corsin aus den Betzdorfer Schichten nebst neuen Beobachtungen an *Pachytheca*. *Palaeontographica Abteilung B*, *97*, 1-38.

Schmitt, D. N., & Juell, K. E. (1994). Toward the identification of coyote scatological faunal accumulations in archaeological contexts. *Journal of Archaeological Science*, *21*(2), 249-262.

Schweitzer, H. J. (1983). Die Unterdevonflora des Rheinlandes. 1. Teil. *Palaeontographica Abteilung B*, *189*, 1-138.

Schweitzer, H. J. (2000). Neue Pflanzenfunde im Unterdevon der Eifel (Deutschland). *Senckenbergiana Lethaea, 80*, 371–395.

Schwimmer, D. R. (1997). Late Cretaceous dinosaurs in eastern USA—A taphonomic and biogeographic model of occurrences. In *Dinofest International Symposium*.

Scott, A. C. (2000). The Pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *164*(1-4), 281-329.

Scott, H.W. (1961). Order Leperditicopida Scott, n. order. Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part Q, Arthropoda 3, 3*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 103–110.

Segerstråle, S. G. (1957). Baltic sea. *Geological Society of America Memoirs*, *67*, 751-800.

Seilacher, A. (1955). Spuren und Fazies im Unterkambrium. In *Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan)* O. H. Schindewolf and A.Seilacher (eds). 373–99.

Seilacher, A. (2007). *Trace fossil analysis*. Berlin, Heidelberg and New York. Springer Science & Business Media.

Seilacher, A., Reif, W. E., & Westphal, F. (1985). Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *311*(1148), 5-24.

Selden, P. A. (1984). Autecology of Silurian eurypterids. *Special Papers in Palaeontology*, *32*, 39-54.

Selosse, M. A. (2002). *Prototaxites*: a 400 MYR old giant fossil, a saprophytic holobasidiomycete, or a lichen? *Mycological Research*, *106*(6), 641-644.

Shear, W. A., Selden, P. A., Gensel, P. G., & Edwards, D. (2001). Rustling in the undergrowth: animals in early terrestrial ecosystems. *Plants invade the land: evolutionary and environmental perspectives*, 29-51.

Sherwood-Pike, M. A., & Gray, J. (1985). Silurian fungal remains: probable records of the class Ascomycetes. *Lethaia*, *18*(1), 1-20.

Shipman, P. (1975). Implications of drought for vertebrate fossil assemblages. *Nature*, *257*(5528), 667-668.

Shipman, P. (1981). *Life history of a fossil: an introduction to taphonomy and paleoecology*.

Siveter, D.J. (1984). Habitats and modes of life of Silurian ostracodes. *Special Papers in Palaeontology*, *32*, 71-85.

Siveter, D. J., Donovan, D. T., Bate, R. H., Robinson, E., & Sheppard, L. M. (1982). Casts illustrating fine ornament of a Silurian ostracod. *Fossil and Recent Ostracods*, *6*, 105-122.

Siveter, D. J., Owens, R. M., & Thomas, A. T. (1989). *Silurian field excursions: a geotraverse across Wales and the Welsh Borderland*. National Museum of Wales in conjunction with Geologists' Association.

Slater, T. S., Duffin, C. J., Hildebrandt, C., Davies, T. G., & Benton, M. J. (2016). Microvertebrates from multiple bone beds in the Rhaetian of the M4–M5 motorway junction, South Gloucestershire, UK. *Proceedings of the Geologists' Association*, *127*(4), 464-477.

Slavík, L., Kříž, J., & Carls, P. (2010). Reflection of the mid-Ludfordian Lau Event in conodont faunas of Bohemia. *Bulletin of Geosciences*, *85*(3), 395-414.

Smith, G. R., Stearley, R. F., & Badgley, C. E. (1988). Taphonomic bias in fish diversity from Cenozoic floodplain environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *63*(1-3), 263-273.

Smith, M. R. (2016). Cord-forming Palaeozoic fungi in terrestrial assemblages. *Botanical Journal of the Linnean Society*, *180*(4), 452-460.

Smith, R., & Kitching, J. (1997). Sedimentology and vertebrate taphonomy of the *Tritylodon* acme zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *131*(1-2), 29-50.

Smith, R. D. A., & Ainsworth, R. B. (1989). Hummocky cross-stratification in the Downton of the Welsh borderland. *Journal of the Geological Society*, *146*(6), 897-900.

Smith, R. M. (1993). Sedimentology and ichnology of floodplain paleosurfaces in the Beaufort Group (Late Permian), Karoo sequence, South Africa. *Palaios*, *8*(4), 339-357.

Southwood, T. R. E. (1985). Interactions of plants and animals: patterns and processes. *Oikos*, 5-11.

Sowerby, J. D. C. (1839). Shells. In Murchison. R.I, *The Silurian System*, 589-712.

Squirrell, H. C. (1958). New occurrences of fish remains in the Silurian of the Welsh Borderland. *Geological Magazine*, *95*(4), 328-332.

Stamp, L. D. (1918). The highest Silurian rocks of the Clun-Forest District (Shropshire). *Quarterly Journal of the Geological Society*, *74*(1-4), 221-46.

Stamp, L. D. (1923). The base of the Devonian, with special reference to the Welsh Borderland. *Geological Magazine*, *60*(9), 385-410.

Stanley, S. M. (1970). Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoirs of the Geological Society of America*. *125*, 1–293.

Stensiö, E. A. (1932). *The cephalaspids of Great Britain*, British Museum. London, 220 pp.

Stensiö, E. A. (1958). *Les cyclostomes fossiles ou ostracodermes. I*: *Traité de Zoologie*, Paris: Masson, *13*(1), 173-452.

Sternberg, C.M. (1970). Comments on dinosaurian preservation in the Cretaceous of Alberta and Wyoming. *Publications in Palaeontology 4*. National Museums of Canada, Ottawa.
Stetson, H. C. (1928). A new American *Thelodus*. *American Journal of Science*, *16*(93), 221-231.

Straw, S. H. (1927). Fish remains from the Upper Ludlow rocks of the Ludlow district. *memoirs of the proceedings of the Manchester literary and philosophy society.*, *71*, 87-91.

Straw, S. H. (1933). The fauna of the Palaeozoic rocks of the Little Missenden boring. *Summary Program of the Geological Survey Great Britain*, *2*, 112-42.

Strickland, H. E. (1852). On a protruded mass of Upper Ludlow Rock at Hagley Park in Herefordshire. *Quarterly Journal of the Geological Society*, *8*(1-2), 381-385.

Strickland, H. E., & Hooker, J. (1853). On the distribution and organic contents of the "Ludlow Bone Bed" in the districts of Woolhope and May Hill. With a note on the seed-like bodies found in it. *Quarterly Journal of the Geological Society*, *9*(1-2), 8-12.

Strother, P. K. (1988). New species of *Nematothallus* from the Silurian Bloomsburg Formation of Pennsylvania. *Journal of Paleontology*, *62*(6), 967-982.

Strother, P. K. (1993). Clarification of the genus *Nematothallus* Lang. *Journal of Paleontology*, *67*(6), 1090-1094.

Suarez, S. E., Brookfield, M. E., Catlos, E. J., & Stöckli, D. F. (2017). A U-Pb zircon age constraint on the oldest-recorded air-breathing land animal. *PLoS ONE*, *12*(6), e0179262.

Sutherland, S. J. E. (1994). Ludlow chitinozoans from the type area and adjacent regions, *Palaeontographical Society Monograph*, *148*(594), 1-104.

Swift, A., & Martill, D. M. (Eds.). (1999). *Fossils of the Rhaetian Penarth Group*. Palaeontological Association. London. pp. 312.

Sykes, J. H. (1977). British Rhaetic Bone-beds. *Mercian Geologist*, 5, 39–48.

Symonds, W. S. (1872). *Records of the rocks; or, notes on the geology, natural history, and antiquities of North & South Wales, Devon, & Cornwall.*

Tanaka, G., Siveter, D. J., & Williams, M. (2019). Devonian shallow marine ostracods from central Japan. *Island Arc*, *28*(1), e12283.

Tarlo, L. H. (1960). The Downtonian ostracoderm *Corvaspis kingi* Woodward, with notes on the development of dermal plates in the Heterostraci. *Palaeontology*, *3*(2), 217-226.

Taylor, E. L., Taylor, T. N., & Krings, M. (2009). *Paleobotany: the biology and evolution of fossil plants*. Academic Press. Elsevier, Burlington, MA. pp. 1230.

Taylor, T. N. (1988). The origin of land plants: some answers, more questions. *Taxon*, *37*(4), 805-833.

Tetlie, O. E. (2006). Eurypterida (Chelicerata) from the Welsh Borderlands, England. *Geological Magazine*, *143*(5), 723-735.

Tetlie, O. E. (2007). Distribution and dispersal history of Eurypterida (Chelicerata). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *252*(3), 557-574.

Tomašových, A., Kidwell, S. M., & Barber, R. F. (2016). Inferring skeletal production from time-averaged assemblages: skeletal loss pulls the timing of production pulses towards the modern period. *Paleobiology*, *42*(1), 54-76.

Torsvik, T. H., & Cocks, L. R. M. (2013). New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. *Geological Society, London, Memoirs*, *38*(1), 5-24.

Torsvik, T.H., & Cocks, L. R. M. (2016). *Earth history and palaeogeography*, Cambridge Cambridge University Press.

Traquair, R. H. (1899). On *Thelodus Pagei,* Powrie, *Sp. from the Old Red Sandstone of Forfarshire*. Robert Grant & Son.

Trinajstic, K. (2001). A description of additional variation seen in the scale morphology of the Frasnian thelodont *Australolepis seddoni* Turner and Dring, 1981. *Records of the Western Australian Museum*, *20*(2), 237-246.

Trueman, C. N., & Benton, M. J. (1997). A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings. *Geology*, *25*(3), 263-266.

Tucker, M. E. (2003). *Sedimentary rocks in the field*. John Wiley & Sons.

Turner, A. H., Brett, C. E., McLaughlin, P. I., Over, D. J., & Storrs, G. W. (2001). Middle–Upper Devonian (Givetian–Famennian) bone/conodont beds from central Kentucky; reworking and event condensation in the distal Acadian foreland basin. Geological Society of America, North-Central Section. In *Abstracts with Programs 33*(4), 8.

Turner, S. (1973). Siluro-Devonian thelodonts from the Welsh Borderland. *Journal of the Geological Society*, *129*(6), 557-582.

Turner, S. (1976) *Fossilium Catalogus I: Animalia. Part 122: Thelodonti (Agnatha)*. Dr W. Junk B.V.'s - Gravenhage, 1-35.

Turner, S. (1986). *Thelodus macintoshi* Stetson 1928: the largest known thelodont (Agnatha: Thelodonti). *Breviora*, *486*, 18.

Turner, S. (1991). Monophyly and interrelationships of the Thelodonti. In *Early vertebrates and related problems of evolutionary biology* (eds). M.-M. Chang, Y.-H. Liu and G.-R. Zhang, Beijing, Science Press, 87-119.

Turner, S. (1999). Early Silurian to Early Devonian thelodont assemblages and their possible ecological significance. In Boucot, A.J., and Lawson, J.D., (eds.), *Paleocommunities: a case study from the Silurian and early Devonian*, Cambridge, UK, Cambridge University Press. 42-78.

Turner, S. (2000). New Llandovery to early Pridoli microvertebrates including Lower Silurian zone fossil, *Loganellia avonia* nov. sp., from Britain. *Courier-Forschungsinstitut Senckenberg*, *223*, 91-128.

Turner, S., Burrow, C. J., Williams, R. B., & Tarrant, P. (2017). Welsh Borderland bouillabaisse: Lower Old Red Sandstone fish microfossils and their significance. *Proceedings of the Geologists' Association*, *128*(3), 460-479.

Ulrich, E. O., & Bassler, R. S. (1923). *American Silurian formations: Paleozoic Ostracoda: their morphology, classification and occurrence*. Johns Hopkins Press.

Valiukevicius, J., & Burrow, C. J. (2005). Diversity of tissues in acanthodians with *Nostolepis*-type histological structure. *Acta Palaeontologica Polonica*, *50*(3).

Varricchio, D. J. (1995). Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *114*(2-4), 297-323.

Varricchio, D. J., Martin, A. J., & Katsura, Y. (2007). First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B: Biological Sciences, 274*(1616), 1361-1368.

Varricchio, D. J., Sereno, P. C., Xijin, Z., Lin, T., Wilson, J. A., & Lyon, G. H. (2008). Mud-trapped herd captures evidence of distinctive dinosaur sociality. *Acta Palaeontologica Polonica*, *53*(4), 567-578.

Vergoossen, J. M. (1995). Remarks on microremains of acanthodians (Gnathostomata) from the Late Pridoli of Manbrook (Upper Silurian; Great Britain). *Geobios, 28*, 399-401.

Vergoossen, J. M. J. (1999a). Siluro-Devonian microfossils of Acanthodii and Chondyrichthyes (Pisces) from the Welsh borderland/south Wales. *Modern Geology, 24*(1), 23-90.

Vergoossen, J. M. J. (1999b). Late Silurian fish microfossils from Helvetesgraven, Skåne (southern Sweden) (I). *Geologie en Mijnbouw, 78*(3), 267-280.

Vergoossen, J. M. (2000). Acanthodian and chondrichthyan microremains in the Siluro-Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential. *Courier-Forschungsinstitut Senckenberg*, 223, 175-200.

Voorhies, M. R. (1969). *Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska*, Contributions to Geology, Laramie: University of Wyoming. *1*, pp. 1-69.

Voorhies, M. R. (1981). Dwarfing the St. Helens eruption: ancient ashfall creates a Pompeii of prehistoric animals. *National Geographic, 159*(1), 66-74.

Voorhies, M. R. (1985). A Miocene rhinoceros herd buried in volcanic ash. *National Geographic Society Research Reports, 19*, 671-688.

Voorhies, M. R. (1992). Ashfall: life and death at a Nebraska waterhole ten million years ago. *University of Nebraska State Museum, Museum Notes, 81*, 1-4.

Vorob'eva, E. I. (2012). Processes of scale formation in fish and Agnatha. *Biology Bulletin*, *39*(2), 99-109.

Waagen, W. (1885) Salt Range fossils; Brachiopoda, *Memoirs of the Geological Survey of India, Palaeontology Indica*, *1*, 329-770.

Walcott, C. D. (1892). Preliminary notes on the discovery of a vertebrate fauna in Silurian (Ordovician) strata. *Bulletin of the Geological Society of America*, *3*(1), 153-172.

Walsh, S., & Naish, D. (2002). Fossil seals from late Neogene deposits in South America: a new pinniped (Carnivora, Mammalia) assemblage from Chile. *Palaeontology*, *45*(4), 821-842.

Warme, J. E. (1975). Borings as trace fossils, and the processes of marine bioerosion. In *The study of trace fossils* by Frey, R. W. (ed.). (pp. 181-227). Springer, Berlin, Heidelberg.

Waters, P. H. (1983). A review of the moulding and casting materials and techniques in use at the palaeontology laboratory, British Museum (Natural History). *The Conservator*, *7*(1), 37-43.

Watson, D. M. S. (1937). II-The Acanthodian fishes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *228*(549), 49-146.

Wehrmann, A., Hertweck, G., Brocke, R., Jansen, U., Königshof, P., Plodowski, G. & Schultka, S. (2005). Paleoenvironment of an Early Devonian land–sea transition: a case study from the southern margin of the Old Red Continent (Mosel Valley, Germany). *Palaios*, *20*(2), 101-120.

Weigelt, J. (1927). *Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung*. M. Weg.

Weigelt, J. (1989). *Recent vertebrate carcasses and their paleobiological implications*. University of Chicago Press.

Wells, J. W. (1944). Middle Devonian bone beds of Ohio. *Bulletin of the Geological Society of America*, *55*(3), 273-302.

Whitaker, J. H. M. (1962). The geology of the area around Leintwardine, Herefordshire. *Quarterly Journal of the Geological Society*, *118*(1-4), 319-347.

White, E. I. (1935). X-The ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *225*(527), 381-457.

White, E. I. (1945). The genus *Phialaspis* and the "Psammosteus limestones". *Quarterly Journal of the Geological Society*, *101*(1-4), 207-242.

White, E. I. (1950). The vertebrate faunas of the lower Old Red Sandstone of the Welsh border*: Pteraspis leathensis* White, a Dittoninan zone-fossil. *Bulletin of the British Museum (Natural History)*, *1*(3), 51-67.

Whittaker, J. E., & Hart, M. B. (Eds.). (2009). *Ostracods in British stratigraphy*. Micropalaeontological Society.

Wigforss-Lange, J. (2007). Tidal facies in the Upper Silurian Öved-Ramsåsa Group of Scania, Sweden: Linkages of radial and cerebroid ooids and evaporite tracers to subtidal, lagoonal environment. *GFF*, *129*(1), 7-16.

Wilson, M. V., & Caldwell, M. W. (1998). The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. *Journal of Vertebrate Paleontology*, *18*(1), 10-29.

Wilson, M. V., & Märss, T. (2009). Thelodont phylogeny revisited, with inclusion of key scale-based taxa. *Estonian Journal of Earth Sciences*, *58*(4), 297-310.

Wilson, M. V., & Märss, T. (2012). Anatomy of the Silurian thelodont *Phlebolepis elegans* Pander. *Estonian Journal of Earth Sciences*, *61*(4), 261-276.

Wolff, R. G. (1973). Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *13*(2), 91-101.

Woodward, A.S. (1891) *Catalogue of fossil fishes in the British Museum. Part II. Containing the Elasmobranchi (Acanthodii), Holocephali, Ichthyodermalites, Ostracodermi, Dipnoi and Teleostini (Crossopterygii), and Chondrostean Actinopterygii*, British Musuem (Natural History), London, 567 pp.

Woodward, A. S. (1904). Notes on the geology and fossils of the Ludlow district. *Proceedings of the Geologists' Association*, *18*(9), 429-442.

Woodward, A. S., & Dixon, E. E. L. (1904). Long excursion to the Ludlow district. *Proceedings of the Geologists, Association*, *18*(9), 487-491.

Woodward, H. (1866)-(1878). A monograph of the British fossil Crustacea, belonging to the order Merostomata. *Palaeontographical Society Monograph*. *32*(145), pp-263.

Zhang, G. R., Wang, S. T., Wang, J. Q., Wang, N. Z., & Zhu, M. (2010). A basal antiarch (placoderm fish) from the Silurian of Qujing, Yunnan, China. *Palaeoworld*, *19*(1), 129-135.

Zhu, M., Yu, X., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., & Zhu, Y. A. (2013). A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature*, *502*(7470), 188.

Zhu, M., & Zhao, W. J. (2009). The Xiaoxiang Fauna (Ludlow, Silurian)-a window to explore the early diversification of jawed vertebrates. *Rendiconti della Società Paleontologica Italiana*, *3*, 357-358.

Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T., & Qu, Q. (2009). The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature*, *458*(7237), 469.

Ziegler, A. M., Cocks, L. R. M., & Bambach, R. K. (1968). The composition and structure of Lower Silurian marine communities. *Lethaia*, *1*(1), 1-27.

Žigaitė, Ž. & Goujet, D. (2012). New observations on the squamation patterns of articulated specimens of *Loganellia scotica* (Traquair, 1898) (Vertebrata: Thelodonti) from the Lower Silurian of Scotland. *Geodiversitas*, *34*(2), 253-271.